HERBAGE REVIEWS

HERBAGE PUBLICATION SERIES

VOL. 7. No. 4.
D E C., 1939.

I·A·B

PUBLISHED BY THE
IMPERIAL BUREAU OF PASTURES AND FORAGE CROPS
ABERYSTWYTH, GREAT BRITAIN

IMPERIAL BUREAU OF PASTURES AND FORAGE CROPS

HERBAGE PUBLICATION SERIES

CORRESPONDING EDITORS

EDITOR: R. O. WHYTE

THE INTERNAL FACTORS OF FLOWERING

N. G. CHOLODNY

Member of Ukrainian Academy of Sciences,
Botany Department, State University, Kiev, Ukraine, U.S.S.R.

(Translated from Russian.)

CONTENTS

1 : INTRODUCTION

AN aspect of exceptional interest in the ontogenesis of higher plants from the point of view of physiology of development would appear to be the transition from vegetative growth to the formation of organs of sexual reproduction, namely, flowers. This phenomenon is accompanied by a clearly expressed metamorphosis of that part of the stem which is to be transformed into a flower; this is also accompanied by some fundamental changes of a cytological nature associated with the initiation and development of a new sexual generation, or gametophyte. No other phase in the entire developmental cycle of a flowering plant exhibits such a sequence of rapid changes, which comprise not only the readjustment of the shoot for the purpose of reproduction, but also leave a deep impression upon the entire physiology of the plant about to flower; these changes induce a number of substantial deviations in the fundamental functions and radical "reconstruction" of the entire plant body.

While all these changes are of great theoretical interest for a physiologist, they naturally at the same time attract the serious attention of practical plant growers. The idea of governing the process of flowering, and hence the fructation of cultivated plants, has long occupied the minds of the most eminent representatives in this branch of our knowledge. Something has, in fact, been achieved in floriculture, horticulture and viticulture, but these achievements, the result of much tedious work, have been based, however, upon occasional observations, upon a blind empiricism, and not upon a precise knowledge and understanding of the processes occurring

NOTE.—The Russian version of this article will appear as part of a book by N. G. Cholodny on "Phytohormones," to be published in the Soviet Union in the near future.

in the plant before and during flowering. The lack of adequate theoretical premises in this research was reflected first of all in its tempo and success. Until recently we have not been in possession of any reliable rational methods of regulating the processes associated with flowering and fructation of plants. Only about 15 to 20 years ago certain trends in the development of methods of mastering that aspect of plant life were first outlined. The starting points were provided by three discoveries which have already made a deep impression (and in future will undoubtedly make a still greater impression) upon the trend, content and conclusions of research in the physiology of development of higher plants. I refer to the discoveries of phytohormones, photoperiodism and vernalization.

Each of these discoveries stimulated the production of scientific papers, the number of which now already approaches several thousands. Each of these discoveries brought to life a new trend in the science of growth and development in the plant kingdom. Although in the beginning these new trends were almost entirely independent of each other, and touched only at some isolated points, they have in our own time begun to approach and flow together into a broad and mighty current, which involves new groups of facts pertaining to the ontogenesis of higher plants. A rapid extension of our factual knowledge makes it possible for us to approach also an attempt at theoretical generalizations which have so far been wanting in this field. The doctrine of phasic development, formulated by Lysenko (Whyte, 1939), and the indications as to the possible participation of phytohormones in ontogenesis are the first steps of the theoretical digest during the last decade in the physiology of development of the plant body. These ideas have naturally left a deep impression upon the entire course of modern research devoted to the physiological cause of the transition of a plant from the vegetative to the reproductive phase of development.

The special features of these more recent investigations, as distinct from the older research of Klebs and other pioneers in the physiology of plant development, consist in that they place in the first rank of importance the question of *internal factors* of ontogenesis, whereas in earlier research chief attention was devoted to those changes in this process which appear as an immediate consequence of the action of various *external factors* upon the plant body.

In the present article I intend to give a brief critical account of the most recent investigations of the internal factors of flowering, in which I shall dwell chiefly upon the investigations of Soviet workers, whose contributions are less known to western European and American botanists.

2: Experimental Evidence

The remarkable phenomenon of photoperiodism discovered by Garner and Allard in 1920, which consists in that some plants flower only in long photoperiods and others in short photoperiods, was until recently most enigmatic in a physiological sense. In other words, we knew nothing of the mechanism which enabled certain photoperiods, that is, a diurnal alternation of daylight and darkness, to speed up flowering in one case, and in the other to retard it, maintaining the plants for an indefinite period in a vegetative state. The first indication as to the direction in which we should look for a physiological explanation of these puzzling facts was received about three years ago, chiefly from the investigations of three Soviet botanists, M. Ch. Čaĭlahjan, B. S. Moškov, and G. M. Psarev. At the same time and probably independently of each other, they all came to the conclusion that the green leaves are the organs which conceive the " photoperiodical stimulus ", and that it is in the green leaves as affected by diurnal alternation of light and darkness of a certain duration that certain physiological processes arise, the action of which then spreads to the

terminal buds, directing them either towards further vegetative growth or towards the initiation and development of reproductive organs. Moškov and Čaĭlahjan made another step forward in quoting some arguments in favour of the idea that the transmission of the photoperiodical stimulus throughout the plant body should be associated with the movements of certain substances from the leaves to the growing point. They both agreed that this substance or substances must be of a hormone nature and thought it possible to speak of a " flower-forming hormone ", to which Čaĭlahjan attached the name of florigen.* Thus, these investigators return to the old conception of Sachs as to the existence of " organ-forming substances ". Kuijper and Wiersum (1936), Melchers (1937), Ljubimenko and Buslova (1937) and some other investigators are also inclined to share this conclusion. As to the question of priority which caused some polemics between Čaĭlahjan and Moškov, in our opinion both these authors contributed equally in their experiments with *Chrysanthemum* to the view that the leaves are the organs which conceive the photoperiodical stimulus. Moškov, however, was the first to begin experiments with this plant, and to indicate the significance of leaves in photoperiodism. Psarev reached the same conclusion with soybean.

The assumption that the " flower-forming substance " manufactured in plants is most probably of the nature of a hormone was put forward, as far as can be judged from their published works, by Moškov and Čaĭlahjan at the same time (1936). Independently and also at the same time, the same idea was advanced by the Dutch investigators, Kuijper and Wiersum (1936).

Čaĭlahjan, who recently published a book entitled " The hormonal theory and plant development " (1937), is perhaps the most ardent and convinced advocate of the " flower-forming hormone " idea. This work is indeed a notable contribution to modern literature on the physiology of plant development ; the questions discussed therein are of great theoretical and practical importance, but at the same time they are not always elucidated in a fair, objective and impartial manner. On the one hand, the author, obsessed by his fundamental ideas, frequently tends to make too hasty conclusions, being satisfied with arguments which on a closer and more objective study of the experimental evidence appear to be rather unconvincing. On the other hand, he neglects at times facts which indeed deserve more serious consideration, but which would hardly, if at all, agree with his fundamental conclusions.

In the first place, it should be pointed out that the title of Čaĭlahjan's book encourages too great expectations, which are in fact left unfulfilled by perusal. We know, particularly after Lysenko's investigations, that every flowering plant passes in its ontogenesis through a sequence of phases, which replace one another consecutively and in a strict rotation. The theory of plant development, no matter what its theoretical bases may be, must of course comprise all these separate links of ontogenesis and must give us the complete scheme of the development of the plant body, beginning with fertilization and terminating in the initiation of new ovaries containing ovules ripe for fertilization. Nothing of this nature is to be found in Čaĭlahjan's book ; it represents in itself only an attempt to explain, in terms of the " flower-forming hormone ", one of the last phases of the ontogenetical development in higher plants, namely, the transition from the vegetative state to the formation of organs for sexual reproduction.

In order to reveal the foundation for the assumption that this transition is effected by a special flower-forming substance acting upon the growing tip, we must

*The name suggested by Čaĭlahjan can hardly be regarded as a happy choice, as it is a compound of Latin and Greek roots; because of an habitual association of ideas (*dermatogen, phyllogen*), it conveys rather the idea of a tissue than of a substance. It would be better to use the name " *anthesin* " derived from the Greek word *anthesis* = flowering.

examine at least briefly the factual evidence furnished by the various investigators. We shall begin with Čailahjan's research.

In most of his studies Čailahjan experimented on short-day plants (*Chrysanthemum, Perilla* and millet). These experiments first of all confirmed the conclusions reached previously by Garner and Allard, Knott, Razumov and others as to the localization of the photoperiodical reaction in those parts of the plant body which were subjected to the effect of short or long photoperiods, the impulse acquired not being transmissible from one branch to another.

This conclusion, however, must not be generalized; as shown by Hamner and Bonner (1938), the photoperiodical stimulus in *Xanthium pennsylvanicum*, a short-day plant, was freely transmitted from one branch to another. Apparently plants differ in this respect and such difference may be related to a larger or smaller production of substances determining flowering; to an unequal facility in their translocation in the tissues of different plants; to the existence of more or less active antagonistic substances and to some other factors.

In order to ascertain which parts of a stem, namely, the leaves or growing tip, conceive the effect of photoperiods, Čailahjan subjected these organs separately to the action of long and short photoperiods. Figure 1 gives an idea of the arrangement of these experiments and the results obtained.

The four plants represented in fig. 1 were decapitated shortly before the experiment was begun. Three of the lateral shoots formed in the upper part of the stem were left on each of the plants intact, but the leaves appearing on the shoots were removed as they arose, at the very beginning of their formation, throughout the

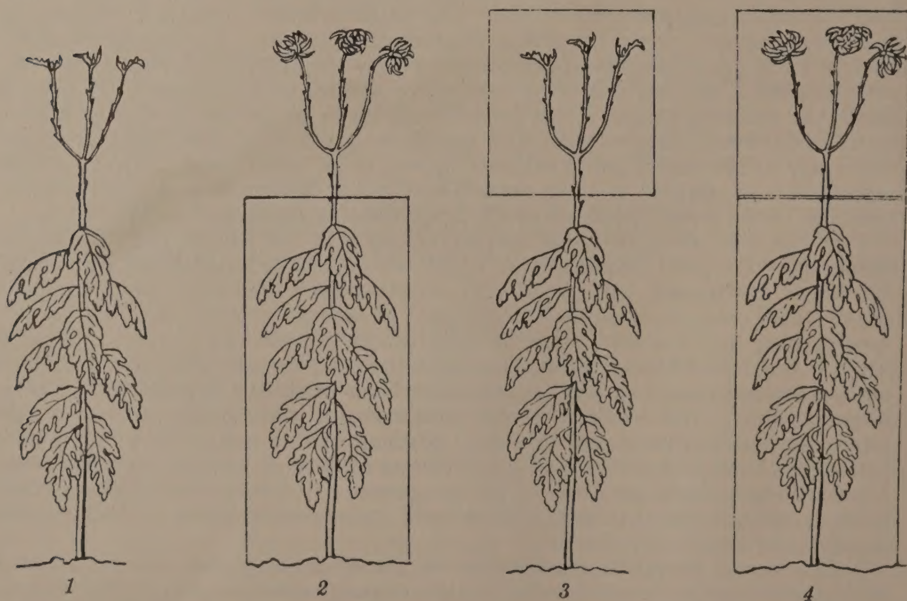

FIG. 1.—Manufacture of "flower-forming hormone" in leaves and efflux to the growing point: upward movement of the hormone, as illustrated by Čailahjan in experiments with *Chrysanthemum* (see pp. 226-7). Reproduced from p. 192 of Čailahjan: "Hormonal Theory of Plant Development" Izd. Akad. Nauk SSSR, Moscow, 1937.

experiment. Several upper leaves were also cut from the main stem. Thus each of the plants was divided into two portions, the upper consisting of the growing tip with a few rudimentary leaves which could not be removed without injury to the growing point, and the lower portion bearing large leaves on the common (main) axis, but without a growing point. The lateral shoots appearing in their axils were removed as they appeared.

The plants thus prepared were subjected to different light environments; the first was left entire in long photoperiods; in the second, the lower portion (with leaves) was subjected to short photoperiods, for which purpose it was periodically darkened with a light-proof sheath; the upper portion (growing point) received long photoperiods throughout. On the third plant, on the contrary, the upper portion was subjected to short photoperiods, while the lower was in long photoperiods. Finally, the fourth plant was grown entirely in short photoperiods. As the drawings show, only the second and fourth plants flowered, the tips of the other two continuing vegetative growth.

The other series of this experiment is shown in Fig. 2. Plants were taken when they began to form deferred shoots (undergrowth). In all, the tips and axillary shoots were removed. One lot (No. 1) was then left entirely in long photoperiods, the other (No. 3) in short photoperiods; in the third group (No. 2), the leaves received

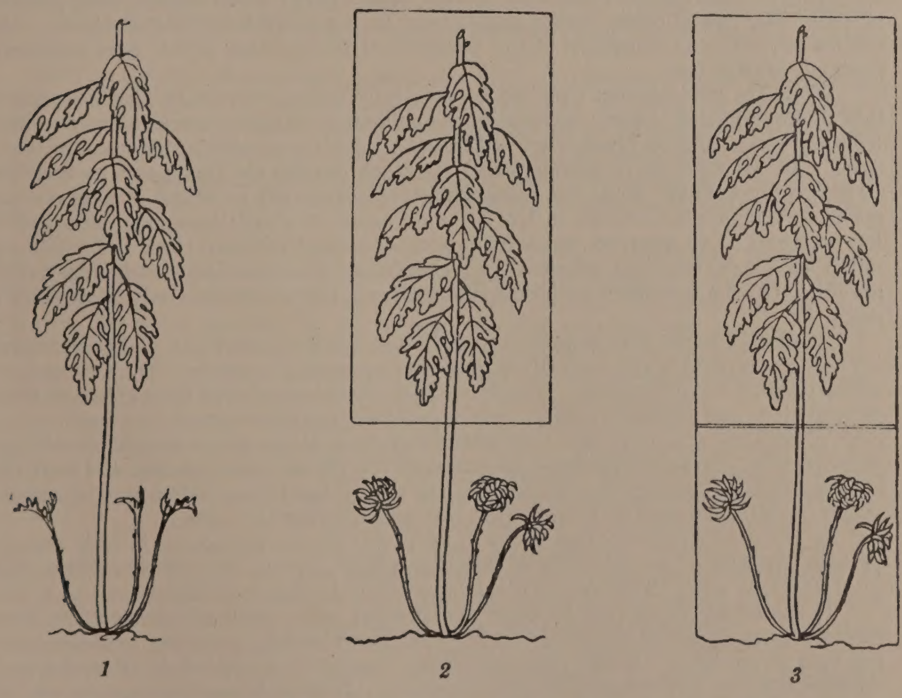

FIG. 2.—Manufacture of "flower-forming hormone" in leaves and efflux to the growing point: downward movement of the hormone as illustrated by Čaĭlahjan in experiments with *Chrysanthemum* (see pp. 227-8). Reproduced from p. 193 of Čaĭlahjan: "Hormonal Theory of Plant Development" Izd. Akad. Nauk SSSR. Moscow, 1937.

short photoperiods, while the deferred shoots remained in long photoperiods. In the latter two groups (as shown on Fig. 2), the deferred shoots flowered and did so simultaneously. The plants of the first group continued vegetative growth throughout the experiment.

If, however, the leaves of decapitated *Chrysanthemum* plants with deferred shoots, but with stems girdled at their basal parts (below the situation of the oldest leaves) were exposed to short photoperiods, the deferred shoots failed to flower. It should be noted that a side incision embracing over half the thickness of the stem, as shown by Čaĭlahjan (1938) in later experiments with *Perilla*, does not prevent the transmission of the photoperiodic stimulus; this may spread not only to the shoots on the intact side, but also on the opposite side as well. Therefore, the photoperiodic stimulus is transmitted both across and along the tissues of the stem.

Čaĭlahjan's experiments with *Perilla nankinensis* are also of great interest. This plant would never flower in the open in the latitude of Moscow (55° 45′ N.) with its long summer days, but it can be forced to flower if grown in 10-hour photoperiods for three or four weeks. Čaĭlahjan used this plant in order to find whether the photoperiodical stimulus can be transmitted from the leaves of one plant to the vegetative tip of another, if, by means of grafting, the tissue of these parts taken from two separate specimens of the same species is induced to unite. For this purpose the tips were cut from several adult *Perilla* plants grown invariably in long photoperiods; the tips of other similar plants were then grafted (in slit) upon them. All the leaves, with the exception of the youngest at the growing point, were removed from the grafted tips.

When the transplanted tips had become fully united, one lot of plants received long photoperiods as before; on some of these plants the axillary shoots were removed from the stock, and on others were left intact; vegetative growth continued in both cases. In the other lot of similar plants the stock bearing the leaves was exposed to 10-hour photoperiods, while the transplanted tips were left as before in long photoperiods. The axillary shoots in this lot were again removed from some plants and left on others. All flowered, but on the specimens which retained the axillary shoots, only these shoots flowered, whereas the transplanted shoots exhibited only vegetative growth. On the specimens without axillary shoots, the scions flowered and prodduce seed.

In another series of experiments with *Perilla*, adult plants which had been grown in short photoperiods and were about to flower were used as stock. The tips and all axillary shoots were removed. Tips from other plants which had been grown in long photoperiods and formed therefore only vegetative organs were used as scions. As a control both the scion and the stock were taken from plants grown invariably in long photoperiods. After the grafting operation all the plants (experimental and control) received seasonal long photoperiods; by the end of the season, when the days grew shorter, additional electric illumination was given during the night.

In these experiments, tips taken from plants grown previously in long photoperiods, but grafted on the stems of flowering plants, eventually began to flower and produced ripe seed. The control plants showed no tendency to flower.

It should be noted that in these experiments, as a result of regeneration, new lateral shoots appeared on the stocks in the leaf axils which, according to the preceding light environment, would have had either vegetative or reproductive tendencies. All these shoots were removed as they appeared. In time, leaves began to appear on the transplanted tips; they were removed in one lot, but left intact in the other. The latter plants were much later than the former in their time of formation of inflorescences and of full flowering; their seeds ripened only partly, and not on all the shoots.

The experiments of the second series suggest that the photoperiodical stimulus

can be transmitted to the transplanted tips even though it had been conceived by the leaves of the stock before the grafting took place, and that this stimulus continues to exert a physiological effect on the growing points of the scion, regardless of the photoperiod in which their development was continued. The presence, however, of young leaves on the transplanted tips grown throughout in long photoperiods probably prevents to a certain extent the manifestation of the photoperiodical induction from the site of the older leaves situated on the stem of the stock.

Later, Čaĭlahjan (1938) described his experiments with grafting *Perilla* plants in which decapitated plants were used as the stock, whereas the scions were the tips taken from flowering plants grown for about a month in short photoperiods. After the grafting, the experimental plants were grown in long photoperiods ; nevertheless, in a fortnight the stock began to form buds, flowered, and produced ripe seed by the end of the experiment. The photoperiodical stimulus could, therefore, be transmitted both from the stock to the scion and conversely.

Other experiments described in the same paper (1938) are of particular interest ; in these, only leaves were grafted on the vegetative *Perilla* plants, that is, plants which had previously been grown in long photoperiods. The tips and all the large leaves were removed from these plants ; later, cuttings taken from flowering plants and consisting of a small portion of stem with a pair of opposite leaves were grafted on the upper portion of the stem. As a control, vegetative plants were used which had been grafted in a similar manner with leaves taken from plants also in a vegetative state.

Both on the experimental and control plants the transplanted leaves became well united and lateral shoots began to appear on the stock ; in the latter lot, however, they retained their vegetative character throughout the experiment, whereas in the former (experimental) plants growth soon ceased and the shoots began to form buds and flowers. Čaĭlahjan therefore concluded that under favourable light conditions a pair of " flower-ready " leaves sufficed to induce metamorphosis of the entire plant, its flowering and fructation.

Čaĭlahjan also repeated the experiments of Gorškov (1929) and Škrebtienko (1932) with *Helianthus tuberosus* and *H. annuus*. The former is a short-day plant and does not flower in the full summer day in the latitude of Moscow (55° 45′ N.). However, when the growing tip of *H. tuberosus* was removed and grafted on the decapitated stem of sunflower plants which were about to form buds or to flower, the grafted tip formed flowers which produced ripe seeds under favourable conditions. The experiments of all these investigators were completely successful.

Another of Čaĭlahjan's experiments which deserves notice is that on the alternating effect of long and short photoperiods upon *Perilla*. Plants received short photoperiods for a month. Shortly before flowering, the tips and all the lateral shoots which also formed inflorescences under short photoperiods were removed. Plants deprived of all fruiting shoots and consisting only of stem and leaves were then exposed to the full natural day, that is, long photoperiods. Soon buds began to appear in the leaf axils, and new shoots were formed. These shoots first began to form only flowers, but later leaves began to appear as well, first small and irregular in shape, but later better developed and normal with large green blades. Thus the fruiting shoots were gradually converted towards the tip into vegetative shoots. If plants with such " mixed " shoots were again exposed to short photoperiods, then the young growing tips of the axillary shoots again began to form flowers instead of leaves. This experiment confirmed the results obtained by Ščeglova with *Perilla ocymoides* and reported by Ljubimenko (1933).

Let us now proceed to Moškov's research. His experiments with *Chrysanthemum* yielded on the whole similar results to those of Čaĭlahjan. It should be noted, however, that Moškov succeeded in establishing more clearly the significance of leaves of

varying ages in conceiving the photoperiodical stimulus. The central four or six leaves proved to be most active in this respect. The younger uppermost leaves which had not yet reached maturity, and the lowest ones which had completed their life cycle were less sensitive to photoperiodic effect. Moškov considered this to be due to a difference in the state of chlorophyll in the leaves of varying ages.

Other interesting experiments made by Moškov include those in which one lot of leaves on the same *Chrysanthemum* plant was subjected to short photoperiods and the other, alternating with the first, was at the same time under continuous illumination, the number of leaves in either lot being the same. These plants formed no flower buds.

Such a result was obtained only in experiments with intact (not decapitated) plants. Sokolovskiĭ, Moškov's co-worker, in experiments with decapitated plants of *Chrysanthemum*, showed that the plants may form buds (on lateral shoots), even in those cases when only one leaf received short photoperiods, while the others were in continuous light; according to Sokolovskiĭ, the time of budding depended upon the number of leaves in short photoperiods, the plants flowering earlier the larger the number of leaves in short photoperiods.

It is necessary also to mention Moškov's experiments on tobacco, which are analogous with Čaĭlahjan's experiments on *Perilla*. Moškov experimented with two tobacco varieties; one of these, Samsun, belongs, as do the majority of forms of *Nicotiana tabacum*, to the long-day group; the other, Maryland Mammoth, to the short-day group. Consequently, when grown in continuous illumination, the former variety forms flowers, the latter only vegetative shoots (Fig. 3, Nos. 2; 1 and 3). The objective was to force the short-day plants, Maryland Mammoth, to flower in

FIG. 3.—Manufacture of "flower-forming hormone" in leaves and efflux to the growing point, as illustrated by Moškov in grafting experiments with Maryland Mammoth and Samsun tobacco (*Nicotiana Tabacum*) (see pp. 230-1). Reproduced from Moškov's paper in ***Trudy prikl. Bot. Genet. Selek.*** Ser. *A*. No. 21. 1937, p. 147.

continuous illumination. For this purpose tips were taken from Samsun plants which had been grown in long photoperiods but had not as yet formed flower buds. These tips were tongue-grafted on to the Maryland Mammoth plants, decapitated 4 to 5 cm. below the tip when they had reached a height of 50 to 70 cm. The Samsun tips were 25 to 30 cm. long and were placed on the stock with a sloping cut made in the lower third. The place of contact was firmly bound with raffia and the free end of the grafted tip was placed in a tube containing water, which was changed daily (Fig. 3, No. 5). Decapitated plants of either variety with Maryland Mammoth tips grafted on to them in a similar manner were used as the control (Fig. 3, Nos. 4 and 7). Further, the experimental series included decapitated Maryland Mammoth plants with short (4 to 5 cm.) Samsun tips grafted in slits on them (Fig. 3, No. 6). In all variants, owing to the decapitation, the plants used as the stock formed lateral shoots which were the primary object of further observation. From the main stems all leaves, except the few lowest ones, were removed to prevent their interference with the development of lateral shoots.

As can be seen from Fig. 3, No. 5, the lateral shoots of Maryland Mammoth plants bearing long Samsun scions formed flower buds two months after the grafting operation. Short scions (4 to 5 cm.) long did not show a similar effect. No trace of flowering was observed on Maryland Mammoth plants bearing the scions of the same variety.

Moškov regards the difference in the physiological effect between long and short scions as due to the fact that the short scions had up to the time of grafting only a few young leaves which had not yet reached maturity and were thus little active, whereas the long scions bore five or six fully developed leaves. The short tips grafted in slits attained in 35 days a size of 25 to 30 cm. only ; probably the time left until the end of the experiment was too short for them to induce changes in development of lateral shoots of Maryland Mammoth stock towards the formation of sexual organs.

The Dutch investigators, Kuijper and Wiersum, published in 1936 results of experiments with soybeans, which were analogous to those of Moškov on tobacco and Čaĭlahjan on *Perilla*. One lot of plants was exposed for about fifty days to short photoperiods (9.5 hours), the other to natural photoperiods (15 to 17 hours). Before the appearance of flowers, the tips of the short-day-grown plants were cut off and grafted on to the stems of long-day-grown plants decapitated at the height of the third or fifth internode. After transference the grafted tips hardly grew, the leaves withered and some were shed. In one case the entire scion was shed in twenty-seven days. The stock, on the contrary, formed vigorous lateral shoots, which produced the first flowers in a month and twenty-four days after the grafting operation. It is interesting to note that on the plant which shed the grafted tip, a flower appeared in one and a half months after the shedding took place.

Melchers (1937) succeeded in inducing flowering in the stock of *Hyoscyamus niger* in the first year of growth, when this biennial race does not normally flower, this effect being produced by grafting flowering scions of the same species, and also of *Hyoscyamus albus*, *Petunia* and *Nicotiana tabacum*.

Later, the same investigator reported other experiments (1939), in which a shortened stem of the rosette of the biennial *H. niger* was used as the stock and one leaf cut from a plant of Maryland Mammoth as the scion. In this case also, flowers were formed on the stock. It is remarkable that a contact for five days between scion and stock was sufficient to induce the transition of the vegetative tip of the stem of *H. niger* from the phase of vegetative to reproductive differentiation : when the tobacco leaves were removed five days after the grafting operation, the stock nevertheless flowered. Some other interesting results reported by Melchers will be discussed later.

These are in main outline the chief facts pertaining to the transmission of the impulse from one part of the plant to another, which is connected with the effect of certain photoperiods on plants, and is probably one of the substantial factors inducing the transition from the vegetative to the reproductive phase.

What is the nature of this impulse? All the investigators quoted above agree that it must have a "physical nature", that is, its origin and transmission are connected with the manufacture and translocation in the plants of a certain substance or substances. In other words, according to the conception of these investigators, those changes in the growing points which lead to the initiation and development of sexual organs occur only in the presence and under the effect of certain substances flowing into the growing point from some other organs of the plant, particularly from the green assimilating leaves.

It must be admitted that such a postulation best explains the experimental evidence described in the preceding pages. If we accept it, it will also follow from this evidence that the substances inducing flowering and manufactured in the leaves are transmitted thence to the nearest growing point, regardless of the distance at which the manufacturing leaves are situated; this transmission may apparently proceed both up and down the stem; the conductive canals are probably situated in the bast; the wood does not participate in the transmission of the "flower-forming substances"; in other words, they move on the whole along with the plastic substances synthesized in the leaves. According to Čaĭlahjan, however, the efflux of the "flower-forming substances" from the leaves may occur not only through the vascular bundles, but also directly in the parenchymatous cells.

Moškov (1937) suggests a possible translocation of these substances from the tissues of the scion into the stock even in the absence of a full union between the grafting components including the vascular bundles. In his experiments with grafting Samsun scions on Maryland Mammoth stocks, "the union between scion and stock was very weak. It was sufficient to remove the raffia and press the scion slightly to separate it from the stock. It was then found that only the outer tissues of the grafted components united, the remainder of the surface of the cuts being covered with dead cells." Nevertheless, in spite of such an apparently weak anatomical union, scions still received considerable amounts of water and mineral salts from the stock. As was noted in the description of the experiments, the scion was first supplied with water from a tube into which the free end was placed. Ten days after grafting, these tubes were removed, and thereafter the scion developed only at the expense of water received from the tissues of the stock. The amount of water and mineral salts taken in this way by the scion was apparently fairly large, as the grafted tips more than doubled in size and flowered during the experiment. This evidence should warn us against Moškov's affirmation as to the absence of a fast anatomical union between the grafted components. This question must be the subject of more careful investigation.

Furthermore, the evidence quoted suggests that it is quite possible that the "flower-forming substances" are not only manufactured, but also stored in the leaves, and that for the transition of plants to the reproductive phase a definite amount of these substances is required; with a deficiency, vegetative growth would continue. The absolute amount of the substances required to induce plants to initiate and develop flowers cannot be very large; this is suggested particularly by the experiments of Kuijper and Wiersum (1936) with the soybean, and also in Čaĭlahjan's experiments (1938) with the grafting of leaves taken from flowering specimens of *Perilla* on to a vegetative stock.

The experiments of Moškov, Čaĭlahjan and Melchers with grafting, in which the scion and the stock belong to plants of different varieties and even of distinct species

and genera, permit us to conclude that " flower-forming substances " are not specific, that is, they are apparently of the same nature in different plants. Moreover, from other experiments made by the same investigators and also by Kuijper and Wiersum, it follows that these substances are probably similar in plants which are distinct in their relation to photoperiods, namely, long-day plants may flower under the effect of substances manufactured by leaves of short-day plants and vice versa. While discussing this problem, it must be borne in mind, however, that the same morphogenetic effect may be induced by the most diverse substances, as has been shown, for example, in recent experiments with induced rooting.

3: The Nature of Flower-Inducing Substances

Let us now return to the problem from which we started, the review of the experimental evidence provided by Čaĭlahjan, Moškov and others, namely, upon what basis should the conception of a hormonal nature of the " flower-forming substances " be founded? As we have seen, the source from which these substances flow to the vegetative tips is the green synthesizing leaves. In photosynthesis, however, very diverse organic compounds are formed in the leaves, which are used as building or plastic materials, and are continuously being translocated from the leaves to the vegetative tips. Involuntarily, the question arises whether these " flower-forming substances " might not belong to the " plastic compounds ". Are they not merely a complex of carbohydrates and nitrogenous compounds which in certain combinations acquire the faculty to promote the initiation and development of floral buds?

In Čaĭlahjan's research (1937), we find only one fact which may be used as evidence against such an assumption. By breaking the bases of *Chrysanthemum* leaves and excising a portion of the main vein 2 to 3 mm. long, Čaĭlahjan observed, nevertheless, that the " flower-forming substances " were still transmitted from the leaf blades to the growing points and " by no means less vigorously than from undamaged leaves ". It should, however, be recalled that in spite of the injury, the leaves of these plants remain throughout the experiment, that is for two months, in a " living and fresh " condition. Hence, it may be concluded that their conductive system was functioning more or less normally and that the influx of the manufactured plastic substances proceeded with sufficient vigour.

Ljubimenko and Buslova conducted similar experiments in 1937 with *Perilla ocymoides*, but obtained different results. They investigated to what extent shortening of photoperiods by darkening the leaves would affect the development of axillary shoots. As it happened, the short 7-hour photoperiods induced earlier flowering of these shoots. If, however, the main vein of the darkened leaves was cut across, the effect of darkening was eliminated ; these investigators ascribed this to the cessation of the efflux of assimilates from the leaves with the excised veins.

Therefore, Čaĭlahjan's experiments with broken *Chrysanthemum* leaves do not yet provide convincing proof of a hormonal nature for the hypothetical " flower-forming substance ". In order to reveal the nature of this substance, that is, to solve the problem whether it is or is not a hormone, experiments must be arranged in such a manner as to prevent the transport from the leaves of the bulk of the plastic substances. More definite conclusions may be made on this point from Melchers' experiments with Maryland Mammoth tobacco leaves grafted on to biennial *Hyoscyamus niger* plants in the first year of growth. During a five-day contact between scion and stock with no fast union between them, there could hardly be transport of any large amounts of plastic substances from the grafted leaves to the tissues or in the opposite direction. An exchange of substances of a hormonal nature would indeed be more likely, as hormones are known to spread easily throughout the plant body, regardless of dissections, in amounts sufficient to manifest their physiological potency.

Some of Moškov's experiments appear to be still more convincing. In *Chrysanthemum*, a short-day plant, grown invariably in continuous illumination and hence maintaining vegetative growth, the blades of the upper four to six leaves were removed ; leaf blades of *Chrysanthemum* plants grown in short photoperiods and hence containing sufficient amounts of " flower-forming substances " were then fixed to the petioles with the help of glass tubes containing water. The transferred leaf blades were changed daily. Some of the plants with leaves thus transferred did, as reported by Moškov, form buds. Under the conditions of these experiments, as also in Melchers' experiments, there could hardly be transference of large amounts of assimilates from the leaf blades to the petioles and stems of the plants. This provides a basis for the interpretation of the results in terms of the hormonal nature of the " flower-forming substances ".

The same may be said regarding recent experiments of Hamner and Bonner (1938) with *Xanthium pennsylvanicum*, the plants of which flower only in short photoperiods (below 15 hours). They could, however, be forced to flower in long photoperiods if sufficiently close contact could be established between the stems of two plants, one of which receives short photoperiods, while the other is in long photoperiods. Hamner and Bonner were successful in doing this by means of a " diffusion contact ". From short portions of the stems of two plants grown prior to the operation in long photoperiods, the bark (as far as the cambium) was removed. The stems were then brought into contact along the injured parts, a thin sheet of paper having already been placed between them ; this would not prevent the diffusion of soluble substances from one stem to the other, but would prevent their union. The place of contact was bound with raffia ; the leaves of one of the plants were then removed and the plants left in long photoperiods ; leaves of the other plants received long photoperiods. Both plants flowered and produced fruit some time later.

All these experiments are sufficiently convincing to show that the substance promoting flowering is of a hormonal nature. It does, however, not necessarily follow that we have to admit the existence of a special " flower-forming hormone ". The leaves are known to manufacture various phytohormones, including in the first place auxin or closely-related compounds which can under certain conditions be elaborated into auxin. In recent years it has been shown that the auxin to which formerly only the faculty of regulating the growth of cells during the elongation stage was attributed is in reality a physiologically multivalent substance. It not only affects growth by changing its rate in one direction or another, but also affects some morphogenetic manifestations, and this is undoubtedly connected with deep-seated changes induced in the tissues by this uncommonly active compound.*

Only a few years ago we observed a curious change of ideas in the study of root-inducing substances. Bouillenne and Went, referring to their investigations (1933) contemplated the possibility of extending Sachs' idea of organ-forming substances to the root initiation of plants. These workers even extracted a substance capable of stimulating this process and named it rhizocalin, that is, a root-forming agent. It was soon found, however, that the initiation and primary development of roots, or at least of adventitious roots, may be induced by most diverse substances, including auxin and heteroauxin. There was, therefore, no need to postulate the existence of a special root-inducing hormone.

We are, of course, not suggesting that Čaĭlahjan's " florigen " will necessarily share the same fate, but the story of rhizocalin is not deprived of an instructive hint : it does suggest that we must form no hasty conclusion regarding special " organ-forming substances " and that we must first test whether some of the already known

*The names " growth hormone " and " auxin " are at the present time obsolete and they do not convey all the diverse physiological properties of these substances.

phytohormones are endowed with the faculty to induce the physiological effect under observation. In the example under discussion, particular care is necessary because there is evidence from the literature that flowering may be speeded up by introducing into the body of some plants substances endowed with the properties of growth hormones. Thus, Hitchcock and Zimmerman (1935), investigating the effect of growth substances on development if introduced through roots, found that when tobacco plants were hormonized through their roots some three to five weeks before the time when the unhormonized plants flower, flowering began much earlier than the normal date. This, however, was not confirmed in the more recent investigations of Murneek (1937). On the other hand, Dostal and Hošek (1937) showed that the excised " flower-ready " stem tips of *Circaea* which ought to flower when grown in cultures began to form vegetative shoots and nodules instead of flowers, if hormonized with heteroauxin.

No matter how contradictory these facts may appear to be at first glance, they do suggest that substances of the growth hormone type are not deprived of the faculty to affect flower formation, and that in the study of this process attention must be given to the problem whether there is any relation whatever with the manufacture of auxin in leaves and other organs.

4: Auxin in Plant Development

The idea of the possible regulative action of growth hormones on the processes relating to the transition of plants from the vegetative to the reproductive state did attract Čaĭlahjan's attention, but was then discarded as a result of a series of experiments. In doing so, however, Čaĭlahjan investigated only one of many possible assumptions. He attempted to investigate whether the transition of plants to flowering is connected in any way with regular changes in the *concentration* of growth hormone in leaves and tips of stems. As the substances stimulating flowering are manufactured in the leaves, it was natural first to investigate whether any changes in the production of growth substances could be detected in these organs in relation to the beginning of sexual development and initiation of flowering. It must be noted that the method of determining auxin in leaves has been fairly clearly elucidated by Avery, Thimann and others, and yields quite reliable results. This method was, however, substantially changed by Čaĭlahjan; using decapitated oat coleoptiles as experimental material, he applied agar blocks containing the hormone not to the upper surface of the cut, but to the side of the coleoptile where the epidermis was intact. Such a modification of the method first employed by Laibach (1935) and Cholodny (1935) is quite acceptable when we are dealing with rich sources of hormones, such as the endosperm of cereal grains, but it can hardly be regarded as appropriate in experiments with leaves where auxin concentration is never as high. It is true that Čaĭlahjan pointed out that, in his experiments, decapitated coleoptiles showed similar curvatures in both cases, that is, when agar blocks containing hormones were placed on the upper surface of the cut or on the side. It is possible, however, to disagree with this conclusion, particularly as it is not supported by any figures and is quoted rather arbitrarily. A comparison of both methods made in our laboratory showed that the method of placing agar blocks on the side is much inferior in its sensitiveness to the common method introduced in physiological practice by Stark and improved by Went and others.

It is, therefore, not surprising that Čaĭlahjan failed to extract growth hormone from the leaves and could not detect it, the experimental and control coleoptiles both showing no curvature.

Discouraged by the first failure, Čaĭlahjan, instead of attempting another more sensitive method, abandoned experiments with leaves altogether and began to com-

pare auxin amounts secreted in the basal parts of cut stem tips of different plants. He then succeeded in establishing that in all plants, whether short day or long day, and regardless of the developmental phase at which they were found (flowering or vegetative growth), the amount of growth hormone was larger the longer the photoperiod experienced by the plants.

This fact as such is not without interest, but has little in common with the question as to the significance of auxin in the processes preparatory to flowering which occur in the green leaves. The fact that in all plants more auxin is secreted from cut tips in long photoperiods than in short photoperiods shows merely that the greater bulk of this substance is not produced in the growing point, as Čailahjan believes, but in the leaves during photosynthesis. It is too presumptuous to attempt to form from these data the conclusion that the growth hormone concentration does not affect the character and trend of development, as we do not know whether there is any proportion between amounts of auxin secreted by basal parts of the cut tips and its concentration in the meristematic cells, where organ-forming processes occur ; and finally, it seems to us altogether groundless to conclude, as Čailahjan did from his experiments, that " flowering and fructation of plants are independent of growth hormones ". This conclusion, as far as it is applied to the formation and development of fruits, conflicts with a number of known facts in modern plant physiology and besides in the part concerning flowering it cannot be regarded as convincing. In Čailahjan's own research we can find some data in support of the assumption that *plants preparing to flower expend on the preparatory processes preceding that most important étape in their ontogenesis a considerable part of the auxin produced by the entire body.* We refer to the experiments with millet (Fig. 4) described by Čailahjan on pp. 22-4 of his book, and conducted to find out " to what extent plants of different ages are sensitive to the effect of photoperiods in speeding up their development ". As millet is a short-day plant, it was subjected to short photoperiods at various consecutive stages of its development, beginning with the appearance of seedlings, for seven days in each case. During all the remaining time before and after the photoperiodic induction the plants grew in seasonal long photoperiods. Thus, counting from the appearance of seedlings, plants were subjected to short photoperiods at ages of from 1 to 7 days in the first group ; 7 to 14 in the second ; 14 to 21 in the third ; 21 to 28 in the fourth ; 28 to 35 in the fifth ; 35 to 42 in the sixth ; 42 to 49 in the seventh ; 49 to 56 in the eighth ; and to full day throughout in the ninth (control). Fig. 4 represents these experimental plants photographed on the 89th day after sowing, August 30. Table 1 summarizes some data concerning the height of plants, total weight of dry matter by the end of the experiment and the time (in days) of flowering.

Table 1.

Age groups :	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
Height of plant (in cm.)	57	72	86	92	55	65	80	84	100
Weight of dry matter (in grm.) per plant	—	3.43	4.84	4.30	3.04	3.54	4.58	4.64	5.18
Time from sowing to the emergence of panicles (in days)	35	35	41	43	43	47	49	52	49

FIG. 4.—The effect of short photoperiods on *Panicum miliaceum* plants of different ages. (See pp. 236.) Reproduced from Čaĭlahjan " Hormonal Theory of Plant Development " Izd. Akad. Nauk SSSR. Moscow, 1937, p. 23.

One cannot fail to notice a remarkable fact in these data. The effect of the photoperiodic induction on the curtailment of growth became gradually weakened from the first group to the fourth, but in the fifth it became suddenly and abruptly stronger, so that plants of that group became and remained inferior in height until the end of the experiment, even as compared with plants of the first group. In the subsequent groups (sixth to eighth) this effect of short photoperiods again became less and less pronounced.

How can this abrupt curtailment of growth in the plants of the fifth group be explained? We find no answer to this question in Čailahjan's theses. He indicated only that the interval between the 28th and 35th days when the fifth group was given short photoperiods " falls just at the period of maximum growth " (apparently in the control). Yet just this note provides a key for understanding the curious phenomenon revealed by Čailahjan.

During the period of intensive growth the plants would, of course, require the largest amount of growth hormones (auxin). A deficient influx of hormones to the zone of growth during that period must provoke an abrupt fall in the eventual height of the plants, as later they would enter such a phase of " the grand period of growth " when the growth rate would fall even under the most favourable conditions, owing to a number of internal causes, and consequently the plants would be unable to make up for the loss. Naturally the question arises whether a cause of the catastrophic fall in height of plants in the fifth group should not be sought in a deficiency of growth hormone. There is no reason to assume that the curtailment of growth could be caused by a deficient supply of plastic substances to the growing organs, as shortening of day length for seven days at the expense of the least bright morning and evening hours could not have a very marked effect on the productivity of the photosynthetic process. Besides, in a month after the appearance of seedlings the plants, while kept in full daylight, should already, and undoubtedly did, accumulate sufficient amounts of reserve substances, at the expense of which they could maintain growth at the required rate, if another factor, which in this case could only be growth hormones, were not at a minimum. And if we see that millet plants receiving short photoperiods when they began their most intensive growth proved to accumulate by the end of the experiment the lowest amounts of dry matter, then this fact should be connected not with a fall in the productivity of photosynthesis, but with a decrease of the assimilating surface as a result of the inadequate increase in size of stems and probably also of leaves on these plants.

If our assumption as to the cause of the curtailment of growth in the plants of the fifth group is correct, a new question arises, namely, what was responsible for such a sudden occurrence of " auxin starvation "? A smaller amount (under short photoperiods) of light energy received could not in this case be of importance for the same reason, as it could not exert itself in the synthesis of organic nutrients. It therefore remains to assume that auxin was inadequate for maintaining growth during that period merely because it was used for other purposes. If we now remember that short photoperiods would have a strong stimulating effect on the processes preparatory to flowering occurring in the leaves, it will be natural to conclude that it was just that preparation in this case for which the auxin reserve was expended, which under other conditions would be used for maintaining growth.

This is the train of arguments which would lead us to conclude that the manufacture of a " flower-forming substance " in the leaves is probably connected with certain chemical transformations of auxin. This supposition gives rise to a number of concrete problems which are quite within the scope of experimental test. And, if further investigations ultimately show that the substance stimulating flowering is of a hormonal nature, it will first be necessary to investigate its relation with auxin.

At the same time, if it were proved that the initiation and development of flowers involves also the participation of special plastic material elaborated in the leaves and transported to the growing point, it should be necessary to investigate the relation between growth hormones and corresponding chemical transformations. In this connexion, we should like to refer once more to the idea first put forward by Tschirch and later carried on by ourselves (Cholodny, 1936), that hormones are regulators of enzymatic processes and that through the enzyme apparatus they may also affect the character of the organic substances manufactured in cells.

Discussing the questions relating to the nature of the photoperiodical induction of *Xanthium*, a short-day plant, Hamner and Bonner (1938) are inclined to think that this phenomenon is connected with more lasting changes in metabolism induced by a short duration of exposure of the leaves to short photoperiods. This stimulation conceived by the plant later continues, in the opinion of Hamner and Bonner, to act under long-day conditions, leading to the manufacture of new amounts of " flower-inducing " substances. This postulation corresponds to that of the synthesis of " flower-forming substances " being an auto-catalytic process.

Since numerous facts have been established to suggest the effect of growth hormones on various morphogenetic processes in the plant body, it is hardly possible to doubt that the ontogenesis of plants as a whole depends to a certain extent on the regulatory activity of these substances. The action of phytohormones on developmental processes, as well as certain other manifestations of their physiological functions, are probably determined by two factors, namely, on the one hand concentration, and on the other qualitative differences, that is, in the first place by their chemical nature and physico-chemical properties. The different physiological effects of the same hormone, for instance, hetero-auxin at different concentrations, have now been established in a good many cases ; it is sufficient, for example, to refer to the growth response of roots, namely, that growth is speeded up with weak concentrations and, on the contrary, is retarded with high concentrations. The role of qualitative differences is also revealed in a comparison of the effect of substances similar in physiological potency, but dissimilar in chemical composition, for instance, hetero-auxin and auxin. The type of response of the plant body to the action of a phytohormone also depends, of course, upon the internal cause, that is, upon the state of the living substratum on which this substance acts, upon its chemical, structural, physiological and other properties.

With the uncommon complexity of all these relations it is possible, of course, to think of such a combination of conditions in which the same substance, for instance, auxin acting upon the meristematic tissues of the growing point, will in one case divert development towards the formation of vegetative shoots, and in the other towards the initiation of organs of sexual reproduction.

While postulating the possible participation of auxin in the processes preparatory to flowering, we do not by any means discard the possibility that some other phytohormones may in one way or another affect these processes. At the present time, it becomes more and more probable that the " regulation " of growth processes and development, that is, various changes in their rate and trend, is a function not of a single substance, but of a complex of substances. It suffices to recall unexpected discoveries during recent years of the significance of various vitamins manufactured in plants ; from a physiological point of view, all these substances should be referred to phytohormones as rightly suggested by Kögl (1937) and others. Involuntarily the question arises whether the " flower-forming substance " is a complex of several phytohormones, for example, auxin and vitamins of group B, which at a definite quantitative ratio acquire the faculty to divert conspicuously the trend of development of embryonic tissues of the growing points towards the initiation of reproductive organs.

With the present state of our knowledge of the physiology of plant development, we have not yet any firm basis for a categorical denial of the possible existence of a special hormone of flowering—anthesin—as a definite chemical entity. We must at the same time emphasize, however, that none of the investigators quoted furnished any convincing proof whatever in favour of the actual existence of such a substance. The most ardent supporter of this idea, Čaĭlahjan, enumerates the differences between the " flower-forming hormone " and auxin, in order to promote the impression of its reality. In his opinion, auxin is manufactured chiefly in the growing points of stems ; the " flower-forming substance " is synthesized in green leaves. Čaĭlahjan considers that the movement of auxin in the plant body is always strictly polar, namely, it spreads only basipetally from tip of stem (or root) towards its base ; the " flower-forming hormone " can be transmitted in all possible directions. In these statements, everything concerning auxin deviates from actual facts. We now know that auxin is manufactured in the leaves during or parallel with photosynthesis. Several examples are now known of non-polar movements of the growth substances and in these cases they probably spread through the elements of the vascular bundles. It is, therefore, presumptuous to speak of differences existing between auxin and the " flower-forming substances ".

We have already said that, in ascribing to the " flower-forming substances " the properties of a special hormone distinct from other phytohormones, Čaĭlahjan goes outside the scope of his own experiments and enters the realm of hypothesis. Unfortunately, this investigator is evidently not conscious of the hypothetical nature of his conclusions. Everywhere he speaks of the " hormone of flowering " as if its existence were a firmly established and unchallenged fact. Actually, we are faced here only with one of many possible hypothetical suppositions which, as we have seen, may be contrasted with another on an equally unsatisfactory basis. All of them can be taken as working hypotheses, absolutely indispensable, of course, in the little known field of physiology of development of reproductive organs, but none can claim anything more than that.

That the procedure connected with the transition from the vegetative to the reproductive phase is very complex and does not fit into the primitive scheme suggested by Čaĭlahjan is demonstrated also in the more recent experiments of Melchers (1939), in the grafting of Maryland Mammoth tobacco plants on the biennial *Hyoscyamus niger* in the first year of growth when they normally form no flowers. As we noted in describing Moškov's experiments, Maryland Mammoth is a short-day plant, and hence no " flower-forming substance " can be formed under long photoperiods. Nevertheless, when a tobacco scion (either entire defoliated stems or leaves alone) grafted on *H. niger* was exposed to long photoperiods, the stock flowered in about the same time as that of the stock of the control, the scion of which was in short photoperiods throughout. It is remarkable that in this case no trace of floral initiation could be found on the grafted stems of tobacco plants grown in long photoperiods. To explain this interesting fact, Melchers resorts to the hypothesis of the existence of another " flower-forming " hormone, " vernalin ", the presence of which is required in plants for the elaboration of Čaĭlahjan's florigen.

Disregarding for the moment the dilemma as to the usefulness of an aggregation of scientific terminology for substances the existence of which has yet to be be proved and which may possibly for ever remain outside real existence like the " unborn souls " in Maeterlinck's " Blue Bird ", we must, however, note that the experiments described by Melchers impel us to conclude that for the transition of plants from the vegetative to the reproductive state, several (at least two) different substances must be present in the tissues, any of which alone does not possess the faculty to induce floral initiation. These experiments may, therefore, be regarded

as an indirect confirmation of the hypothesis put forward by us earlier, that the initiation of organs of sexual reproduction is determined by the action upon embryonic tissues of the vegetative tip, not of a single specific "flower-forming substance" alone, but of a certain complex of phytohormones (auxin, vitamin B, and others). Such a supposition is more probable since different plants and the same one plant are endowed, as we now know, at different phases of development with a different faculty to synthesize and accumulate hormones or vitamins. It is possible, therefore, that in the growing tips of the biennial *H. niger* the organs of sexual reproduction are not laid down in the first year of development, because one or several links in the complex of phytohormones required for flowering are lacking. On the other hand, it is just these substances necessary for flowering which are present in sufficient amounts in the tissues of the tobacco scion and which are transmitted to the tissues of the stock. The scion probably requires some other substances which it cannot form in long day and which cannot be supplied by the stock.

During recent years, different investigators have made numerous attempts to induce flowering in vegetative plants by treating their tissues with various substances of the vitamin and hormone groups. The experiments of Hamner and Bonner (1938) with *Xanthium* were made on a particularly extensive scale. They tested various solutions of vitamins B_1, B_2 and B_3, ascorbic acid, nicotinic acid, pantothenic acid, theelin, theelol, inositol and heteroauxin (indole-acetic acid). None of these compounds could induce even the initial manifestations of reproductive development. These negative results, however, do not in any way conflict with the supposition that for such a change in plant development an influx of several active substances in certain combinations to the vegetative tips is required. To compound such a mixture is not an easy task and as far as we are aware no experiments in this direction have yet been undertaken.

5 : The Environment and Manufacture of Flower-Inducing Substances

In discussing questions pertaining to the nature of the photoperiodic response of plants, yet another aspect must at least be briefly touched upon. We have already mentioned that, according to data furnished by Moškov and Čaĭlahjan, the "flower-forming substance " manufactured in the leaves under the effect of certain photoperiods, longer for long-day and shorter for short-day plants, is of the same kind in both groups. If this is so, why do different plants require different photoperiods for the transition from vegetative growth to flowering ?

Čaĭlahjan considers that the " hormone of flowering " is synthesized in the leaves under the effect of solar energy, but at the same time he states that this substance " originates under that duration of diurnal light to which the species in question was adapted : the plants of tropical and subtropical countries flower and fruit in short photoperiods, and the plants of higher latitudes in long photoperiods ". Such a conception, however, is not in agreement with our knowledge of photochemical reactions. In fact, if we are to accept this point of view, we have to admit that the substance originating in the leaves of short-day plants under a 10-hour photoperiod disappears completely without leaving a trace when given a small additional illumination ; and, on the contrary, in the leaves of long-day plants, exactly the same compound is not formed in 10-hour exposures to light, but suddenly appears with a small increase in the duration of diurnal illumination. All this is hardly, if at all, plausible. Would it not be simpler to assume that the " flower-forming substance " is synthesized in leaves under any duration of day and night, but that, under the effect of photoperiods, this substance is not formed in equal amounts and that, on the other hand, different amounts are required by long-day and short-day plants to complete

their preparation for flowering and the change-over to the reproductive phase of development ?

Another supposition would be just as good, namely, that for flowering either group of plants requires the same amount and concentration of " flower-forming substance ", but that the rate of accumulation in the leaves is not the same in long-day and short-day plants ; its elaboration may be slower in the former and they may therefore need longer durations of light.

These two suppositions, however, do not exhaust all the possible hypotheses. It must not be overlooked that the chemical composition of plants depends not merely upon those processes which take place in leaves exposed to light and for which light is indispensable as a source of energy, but also upon those processes which proceed in darkness. These include the typical " dark reactions ", that is, those which may progress normally only in the absence of light—because the substances formed in these reactions are readily oxidized or destroyed in light. It is quite possible that in short-day plants the " dark reactions " are decisive in their photoperiodism. In support of this suggestion may be quoted the well-known experiments of Lysenko (1932) with millet and other short-day plants. Lysenko showed that millet may attain flowering not only in long photoperiods, but even in long continuous day, if slightly germinated seeds of that plant were treated with darkness for five days at 25—30°C. and in reduced moisture conditions (26 parts of water to 100 parts of seed by weight). Seeds thus " vernalized " do not any more require " short-day " in order to accomplish all the subsequent phases of their development. The same method, according to Lysenko, is applicable to soybean, Sudan grass and sorghum.

As far as can be judged from these data, the photoperiodic stimulus, in at least some short-day plants, may be replaced by the continuous dark treatment of growing embryos for a few days. In Lysenko's opinion, we should speak not of plants of long or short day, but of plants requiring light or darkness for the completion of a definite phase in their development.

It is rather difficult to co-ordinate Lysenko's conclusions with some of Moškov's results with *Chrysanthemum* (1939). When this plant is given 10 short (10-hr.) days, subsequently it flowers even in continuous day. Since during this 10-day period the experimental plants received 140 hours of darkness, an attempt was made to replace the action of ten short photoperiods with continuous darkness for 3 to 12 days, the plants being transferred subsequently to continuous light. The experiments were made with both entire plants and isolated leaves ; in the latter case the duration of the dark treatment was continued up to two months. In no case in this experiment did the plants flower. Therefore, the action of darkness was not equivalent to the action of an alternation of light and dark periods.

An uncommon refinement and specialization of photoperiodic response in some plants was also shown in the same report of Moškov by the data concerning the physiological significance of small differences in the length of photoperiods (about 10 to 20 min.) when the latter approached the critical, that is, the shortest and the longest durations at which the plant is still capable of initiating reproductive organs.

If we are to accept the above-mentioned point of view of Lysenko, the most decisive part (in the sense of regulating development) in the chemistry of short-day plants must be played by " dark reactions " and conversely by " light reactions " in long-day plants.

The experiments of Hamner and Bonner (1938) with *Xanthium pennsylvanicum* are of particular interest in this connexion. The critical photoperiod for this plant is about 15.5 hours and the critical period of darkness is accordingly 8.5 hours. These investigators decided to study the factor which determines floral initiation in *Xanthium*, namely, whether it is photoperiods or darkness. If the first supposition

is correct, the flowers must obviously be laid down in any photoperiod shorter than 15 hours, and, on the contrary, no flower will appear in any photoperiod longer than 15 hours, regardless of the duration of the dark period. If, however, the initiation of organs of sexual reproduction is determined by the duration of the dark period, the plants will form flowers in any period of darkness exceeding 8.5 hours and persist in a vegetative state in shorter periods of darkness, regardless of the photoperiod accompanying them. As it was previously found that *Xanthium* flowered profusely in a 24-hour cycle, including an 8-hour photoperiod and 16-hour darkness, two other cycles were tested with the same ratio between light and dark periods (1 : 2), namely, 12-hour cycles consisting of a 4-hour photoperiod and an 8-hour dark period, and 48-hour cycles, including a 16-hour photoperiod and 32-hour dark period. It was then found that plants failed to flower and remained in a vegetative state in a 4-hour photoperiod and 8-hour darkness, but that they soon flowered profusely in a 48-hour cycle with the same ratio between light and darkness. Therefore, prolonged photoperiods, when accompanied by adequately long " nights ", did not prevent *Xanthium* (a short-day plant) from flowering.

Subsequent experiments of Hamner and Bonner with *Xanthium* showed that at 21-27°C. a single prolonged darkening (15 hours) with a subsequent short photoperiod (9 hours) was sufficient to induce floral initiation in long photoperiods.

All the experimental data quoted by Hamner and Bonner lead to the conclusion that " the flowering response of *Xanthium* to short photoperiods depends primarily upon reactions directly related to the dark period " and that consequently biochemical reactions in leaves of that plant, which lead to the synthesis of substances inducing flower initiation, occur not in the light but in the dark.

Only more or less hypothetical suppositions are possible with regard to the nature of all these reactions, both photochemical and " dark ". For short-day plants, light, as we have noted, may acquire the significance of a factor promoting the destruction or oxidation of the active compounds formed in darkness. On the other hand, in leaves exposed to light, certain compounds may arise which may inactivate the " flower-forming substance " manufactured by the same or other leaves in darkness. The existence of such substances antagonistic to substances determining flowering was confirmed in some experiments of Hamner and Bonner. At the same time, the prerequisite for flowering in short-day plants may also be the absence or reduced concentration of phytohormones formed in light. Roodenburg (1937) pointed out, in connexion with Lysenko's experiments with millet, that the amount of auxin in plants falls in darkness and rises in light. In his opinion, this may be connected with the changes in development under the effect of long and short photoperiods.

The very diversity of the possible suppositions in this field suggests how far we are from any satisfactory decision as to the nature of the biochemical and physiological reactions connected with the effect of photoperiods on plants. No matter how this question will be solved in the future, it is necessary to remember that at the basis of the different photoperiodic response of different plants there lies their hereditary constitution, particularly their genotype, formed in the evolution of the species in question in accordance with the natural-historical conditions of its existence.

6: Physiological Cause of Vernalization

The acceleration of flowering in short-day and long-day plants under the effect of appropriate photoperiodic induction has, undoubtedly, a good deal in common with the shortening of the vegetative period in annual plants which may be induced by the so-called vernalization. The latter, as is known, consists of more or less

prolonged treatment of growing seeds or young plantules somewhat advanced in growth with a definite complex of external factors, among which temperature is of outstanding importance. At a first glance, however, there would appear to be a substantial distinction between these two manifestations, namely, the photoperiodic stimulus is conceived, as we have seen, in the leaves, whereas in vernalization, regardless of the phase of growth at which it is effected, the entire plant body is subjected to the effect of the appropriate complex of external factors.

This difference, however, will not appear to be so great if it is remembered that the photoperiodic stimulus, as suggested by all the above-mentioned investigators, consists ultimately in the action of certain substances on the embryonic tissues of the growing point, that is, upon the same part of the plant body in which, according to modern conceptions, the changes associated with vernalization are also localized.

On the other hand, every growing point in higher plants, regardless of its situation, must pass through definite stages of development, following one another regularly in the same way as the entire body of an annual plant develops from seed embryo. As the ontogenesis would reflect to a certain extent the phylogenesis of the species in its consecutive *étapes*, in all plants which have passed along the same evolutionary path, different phases of ontogenesis must be similar in their main outlines and must follow one another in the same hereditarily determined order. Roughly speaking, this order is expressed in the alternation of generations (sporophyte and gametophyte), and in the fact that every embryo and every bud form during development first vegetative and then reproductive organs (if the latter are formed at all).

This historically settled and hereditarily fixed ontogenetic cycle requires, of course, definite external and internal conditions for its normal development. At every developmental phase, plants generally require different conditions, and these consecutive changes in the "requirements" of an organism with regard to the external and internal environment, just as all other characters of its ontogenesis, would appear to be the result of long evolution and to have an adaptive nature.

According to the now generally accepted conceptions based chiefly upon Lysenko's research, annual plants at the beginning of their development pass through two developmental phases, namely, the stage of vernalization (or the thermo-phase) and the photo-phase. During the second phase, the determinative role (among the external factors affecting further development) is played by light. It is in this phase that the plant probably acquires the faculty to conceive the effect of the photoperiodic stimulus. This may be regarded as established as far as long-day plants are concerned.

Opinions differ as regards the significance of light to short-day plants. If we adopt Lysenko's point of view as discussed above, the question arises whether in general for them the significance of light affecting their ontogenesis does not consist merely in supplying the plant body with the necessary photosynthetic energy. Thus the existence of a photo-phase in the development of plants of this group would probably be challenged. Such an assumption is very unlikely.

According to other views, short-day plants, just as long-day plants, require for their normal development a photoperiodic impulse in the form of photoperiods of a definite length and they become sensitive to this impulse only after the appearance of the first leaf. We shall note also that, according to Whyte and Oljhovikov (1939), no difference in principle exists between long-day and short-day plants: both types in the beginning of their development pass through three consecutive phases, namely, thermo-phase, dark-phase and light-phase. In the opinion of these investigators, the differences found in the literature are due chiefly to the fact that short-day and long-day plants have been compared at different developmental phases, namely, the

dark-phase of the short-day plants has been contrasted with the light-phase of long-day plants.

If the complex of operating external and internal factors during an ontogenetic phase does not correspond to the historically settled " norms " and " requirements " of a plant, more or less profound changes in ontogenesis would take place. These changes would more commonly be concerned with the length of the developmental phases and less frequently with their hereditarily determined sequence. The prolongation of the stage of vegetative growth in winter cereals when deprived of the effect of low temperatures required during their early development is a classic example of this type of change. In perfect analogy with this phenomenon is the delay in the initiation and development of organs of sexual reproduction (flower) in short and long-day plants when exposed to photoperiods contrary to their requirements. Therefore, from the evolutionary standpoint, photoperiodism and vernalization may also be referred to the same one group of phenomena.

The question arises whether we should not see in this similarity the manifestation of deeper organic connexions between photoperiodism and vernalization, an evidence of a certain likeness in their physiological nature. Physiological analysis of photoperiodism leads us, as shown in the investigations described in this review, to an assumption that at the basis of this phenomenon there is an action of certain substances on the growing point. Could this assumption be extended to those changes in the growing point which are associated with vernalization ?

This question was first put forward by the writer long before any detailed studies of photoperiodism had led some investigators to the conceptions discussed in the earlier parts of this review. An attempt to approach the interpretation of changes in ontogenesis of annual plants from the point of view of phyto-endocrinology was made independently of the investigations of photoperiodism, while studying the " hormonal system " of germinating seed of cereals (1935).

As recent investigations show (Schander, 1934 ; Cholodny, 1935 ; Laibach, 1935, and others), seeds contain reserves of various phytohormones received from the mother plant and concentrated chiefly in the endosperm or cotyledons. This reserve comes into action during germination, and at early stages of this process the phytohormones of the endosperm (cotyledons) are transmitted to the organs of the embryo beginning growth and development. Cereals have been more fully studied in this respect than any other plants. Schander (1934) showed that the active substances contained in grains at the very beginning of germination pass over to the embryo through the special elongated cells of the aleurone layer. These substances, according to Schander, are required for further development and growth of the embryo. Cholodny (1935) found that auxin, or a related compound, accumulated in the endosperm during germination of cereal grains, is also transmitted into the embryo. On the other hand, Cholodny also investigated the effect of increased concentrations of phytohormones contained in the endosperm on the meristematic cells of roots and concluded that the rate of cell development is thus accelerated considerably.

All these investigations were used as the basis of a hypothesis advanced by the writer in 1936, which was the first attempt to reveal the nature of the " internal factors " acting upon the growing points of the plants during vernalization. Awakened to life, but lacking the possibility of normal growth (as a result of insufficient moisture and low temperature), the embryo of the vernalized seed absorbs from the endosperm the growth hormones contained there in great quantity. Inasmuch as this substance is expended principally in growth, and since under the conditions of vernalization there was almost no growth, the concentration of the hormone in the cells of the embryo rises considerably above the norm. Increase of the intra-

cellular concentration of the hormone in the growing points causes an acceleration of the passage of the meristem cells of the young plant through the first phases of development, according to their hereditarily determined sequence. In this way, the interval of time that separates these first phases of development from its later stages, connected with preparation for fruiting, is shortened. The result is that the whole cycle of the plant development is finished sooner than it would be under normal conditions (Cholodny, 1936).

The first attempt to check the correctness of this hypothesis was made by Konovalov (1937). He subjected the excised embryos of Ukrainka winter wheat to vernalization. Seeds were soaked to acquire 50 per cent moisture; three hours after imbibition the embryos were separated from the endosperm by means of a razor and then vernalized on a 3 per cent sugar solution at 2 to 3°C. for 46 days. As the experiments were not carried out under sterilized conditions, a large number of the excised embryos perished. From the remainder some 8 per cent could be grown successfully into normal plants, which eared in the same year only about 15 days later than the control plants derived from intact seeds normally grown and vernalized under the same conditions of temperature and moisture. Proceeding from these experiments, Konovalov concluded that vernalization of embryos can be effected without any participation of the endosperm and that the latter acts merely as an organ supplying nutrients to the embryo.

This conclusion, however, could hardly be considered convincing, as the embryos were separated from the endosperm a few hours after imbibition of the seed. In the interval, a considerable amount of the phytohormones of the endosperm could have entered the embryo tissues. As shown by Schander, a few hours was sufficient for the embryos of imbibed seeds to receive the required " hormone charge ", thus promoting their development into normal plants.

A similar method—growing plants from excised and then vernalized embryos—was employed by Gregory and Purvis (1938), but these investigators sterilized the seeds of winter rye before the operation and then cultivated them on nutrient agar under sterilized conditions. The plants derived from excised embryos which were vernalized after separation from the endosperm eared at the same time as the control from seeds vernalized intact. It should, however, be borne in mind that Gregory and Purvis sterilized seeds by soaking them for 5 hours in a solution of calcium hypochlorite containing 1 per cent chlorine. Therefore, in their experiments as in that of Konovalov, the enrichment of embryos with phytohormones at the expense of their reserves in the endosperm must have already occurred. Foreseeing this objection, Gregory and Purvis pointed out that imbibition of all seeds in a sterilizing solution was made at room temperatures, regardless of whether the embryos were later excised or not and whether they were vernalized or not. Therefore, the transmission of phytohormones into the embryo, in their opinion, could not be the cause of the difference in the subsequent development of the plants from vernalized and unvernalized embryos. In their opinion, the most probable cause of the differences lies in the different effect of low temperatures on the subsequent action of the hormone which entered the embryo from the endosperm.

Discussing further the postulation put forward by the writer that the accumulation of phytohormones in vernalized embryos may be responsible for accelerating their development, Gregory and Purvis referred to some earlier data of Purvis (1934) from which it does follow, in their opinion, " that up to the stage of flower initiation developmental processes go on at the same rate in vernalized and unvernalized plants; thus, the leaf production rate is the same and there is no indication of earlier senescence in individual leaves in vernalized plants."

As regards this last note, it should be pointed out that the authors seem to confuse growth and development ; thus accelerated " ripening " may or may not be accompanied by accelerated growth of vegetative organs. In addition, Purvis' data may be contrasted with some later observations of Sereĭskiĭ and Sludskaja (1937) which revealed an unmistakable acceleration in the development of seedlings of spring and winter wheat following vernalization.

As regards the experiments of Gregory and Purvis with excised embryos, they do not, in our opinion, contradict our hypothesis. Indeed, if we admit that during the first five hours when seeds were soaked in the sterilizing solution, the concentration of phytohormone was increased due to absorption from the endosperm, later, this concentration, which was at first equal in all seeds, could not remain at the same level in vernalized and unvernalized embryos ; it ought to decrease rapidly in the latter, due to the expenditure of growth substances in growth, whereas in the former, in the absence of or at a reduced rate of growth, all the initial amount of these substances should remain unchanged. Since the process of development does not depend upon the rate of growth and is maintained throughout the period of vernalization, it is obvious that unequal intracellular concentration of phytohormones might also affect any subsequent development of vernalized and unvernalized plants under the conditions in which the experiments of Gregory and Purvis were conducted.

From these experiments it should, in our opinion, be concluded that, apart from phytohormone concentration, the development of the embryo must be affected also by the *duration* of the action of these substances. This conclusion has indeed been confirmed by Thimann and Lane in a recent paper (1938).

A rapid advance of our knowledge of phytohormones during recent years impels us to introduce yet another correction to our initial hypothesis. It is hardly possible at the present time to doubt that the *qualitative aspect* of the complex of phytohormones acting upon the embryo is not also without its own effect upon the development of the embryo. The composition of that complex and the chemical nature of the active substances found in tissues of the embryo and of the plant developing from it undoubtedly change also under the effect of the external and internal conditions in which development is maintained.

Therefore, the experimental evidence published by various investigators during recent years provided no basis for considering our hypothesis of the physiological cause of vernalization to be as inconsistent as stated by Gregory and Purvis ; it compels us merely to make certain corrections in this hypothesis.

That the postulation proposed by us may be useful as a working hypothesis is testified by some of our experiments with pre-sowing treatment of seed with various solutions of heteroauxin and blastanin (Cholodny 1936), as well as by some later experiments by Thimann and Lane (1938) and also by Čaĭlahjan and Ždanova (1938). All these investigators found that a short treatment of growing seeds with increased concentrations of phytohormones affected subsequent development of plants. In some cases it was observed that the growth of vegetative organs was accelerated ; in others fructation was intensified and occasionally conspicuous curtailment of the vegetative period was recorded. These data are still preliminary and indeed require revision and supplementary investigation, but they nevertheless make it possible to hope that the introduction of phytohormones into the plant body at different stages of its development may in future prove to be a useful method of increasing the productivity and of regulating the development of agricultural plants.

References

1. Avery, G. S. *Bull. Torrey bot. Cl.* Vol. 62. 313-30. 1935.
2. Bouillenne, R., and Went, F. *Ann. Jard. bot. Buitenz.* Vol. 43. 25-202. 1933.
3. Čaĭlahjan, M. Izd. Akad. Nauk SSSR. Moskva. 198 pp. 1937.
4. ———— *C. R. Acad. Sci. URSS.* Vol. 18. 607-12. 1938.
5. ———— and Ždanova, L. *C. R. Acad. Sci. URSS.* Vol. 19. 303-6. 1938.
6. Cholodny, N. G. *Planta.* Vol. 23. 289-312. 1935.
7. ———— *C. R. Acad. Sci. URSS.* Vol. 3 (12). 391-4. 1936 (a).
8. ———— *Priroda, Moskva.* No. 3. 79-92. 1936 (b).
9. ———— *Priroda, Moskva.* No. 2. 36-47. 1937.
10. Dostal, R., and Hošek, M. *Flora* N. F. Vol. 31. 263-86. 1937.
11. Garner, W. W., and Allard, H. A. *J. agric. Res.* Vol. 18. 553-606. 1920.
12. ———— *J. agric. Res.* Vol. 31. 555-66. 1925.
13. Gorškov, I. S. *Trudy gos. bot. Pitomnika im. Mičurin.* 1929.
14. Gregory, F. G., and Purvis, O. N. *Ann. Bot., Lond.* n.s. Vol. 2. 237-51. 1938.
15. Hamner, K. C., and Bonner, J. *Bot. Gaz.* Vol. 100. 388-431. 1938.
16. Hitchcock, A. E., and Zimmerman, P. W. *Contr. Boyce Thompson Inst.* Vol. 7. 447-76. 1935.
17. Knott, J. E. *Proc. Amer. Soc. hort. Sci.* Vol. 23. 67-70. 1926.
18. Kögl, F. *Naturwissenschaften.* Vol. 25. 464-70. 1937.
19. Konovalov, I. N. *C. R. Acad. Sci. URSS.* Vol. 16. 381-3. 1937.
20. Kuijper, J., and Wiersum, L. K. *Proc. Nat. Acad. Sci. Amsterdam.* Vol. 39. 1114-22. 1936.
21. Laibach, F., and Meyer, F. *Senckenbergiana.* Vol. 17. 73-86. 1935.
22. Ljubimenko, V. N. *Sovet. Bot.* No. 6. 3-30. 1933.
23. ————, and Buslova. *C. R. Acad. Sci. URSS.* Vol. 14. 149-52. 1937.
24. Lysenko, T. D. *Bull. Jarov.* Nos. 2/3. 16-34. 1932.
25. Melchers, G. *Biol. Zbl.* Vol. 57. 568-614. 1937.
26. ———— *Ber. dtsch. bot. Ges.* Vol. 57. 29-48. 1939.
27. Moškov, B. S. *Trudy prikl. Bot. Genet. Selek. ser. A.* No. 17. 25-30. 1936.
28. ———— *Trudy prikl. Bot. Genet. Selek. ser. A.* No. 19. 107-26. 1936.
29. ———— *Trudy prikl. Bot. Genet. Selek. ser. A.* No. 21. 145-56. 1937.
30. ———— *Sovet. Bot.* (in press). 1939.
31. Murneek, A. E. *Res. Bull. Mo. Agric. Exp. Sta.* 268. pp. 84. 1937.
32. Psarev, G. M. *Sovet. Bot.* No. 3. 88-91. 1936.
33. Purvis, O. N. *Ann. Bot., Lond.* Vol. 48. 919-55. 1934.
34. Razumov, V. I. *Trudy prikl. Bot. Genet. Selek.* Vol. 27. No. 5. 249-82.
35. Roodenburg, J. W. M. *Ber. dtsch. bot. Ges.* Vol. 55. 5-32. 1937.
36. Schander, H. *Z. Bot.* Vol. 27. 433-515. 1934.
37. Sereĭskiĭ, A., and Sludskaja, M. *C. R. Acad. Sci. URSS.* Vol. 17. 55-8. 1937.
38. Škrebtienko, T. *Semenovodstvo.* Nos. 17/18. 25-7. 1932.
39. Thimann, K. V., and Lane, R. H. *Amer. J. Bot.* Vol. 25. 535-43. 1938.
40. Whyte, R. O. *Biol. Rev.* Vol. 14. 51-87. 1939.
41. ————, and Oljhovikov, M.A. *Nature, Lond.* Vol 143. 301-2. 1939.

THE COMPARATIVE VALUES OF THE FAIRWAY VARIETY AND THE STANDARD TYPES OF CRESTED WHEAT GRASS

T. M. Stevenson

Dominion Agrostologist, Division of Forage Plants, Central Experimental Farm, Ottawa, Canada

and

W. J. White

Assistant in Plant Breeding

Dominion Forage Crops Laboratory, Saskatoon, Sask. Canada.

This article is a reproduction of a circular prepared by the Division of Forage Plants, Ottawa, in response to numerous requests for information regarding the comparative values of Fairway and the so-called standard types of crested wheat grass. A short bibliography of references in the Imperial Bureau of Pastures and Forage Crops has been added. This is not intended to be complete; much fuller information can be obtained by reference to the Index of Genera supplied with each quarterly issue of *Herbage Abstracts* and in the annual indexes of *Herbage Abstracts* and *Herbage Reviews*. Numerous references to the study and use of crested wheat grass in the western States of U.S.A. are made in Bulletin 26 of this Bureau (September 1939).—R.O.W.

There appears to be an unfortunate impression abroad that the Fairway variety of crested wheat grass (*Agropyron cristatum*) produced at the Dominion Forage Crops Laboratory, Saskatoon, Saskatchewan, is suited primarily for lawn purposes rather than for general farm production. This has resulted, no doubt, from the fact that the Fairway variety has been recommended as a suitable grass for farm lawns, school yards, and golf fairways under dry-land conditions, and where artificial watering is not practised. Its usefulness for these purposes is due to its superior tillering capacity, as compared with the standard types, which results in a relatively dense turf as well as to the fact that it is finer of stem and somewhat more leafy.

Nevertheless, data which have been obtained from a large number of tests conducted over a period of years indicate that the Fairway variety has much to recommend it, in preference to the standard types, for general farm production as well as for dry-land lawns.

Table 1.—Average Yield of Hay

Description of Tests	Period covered by tests	Yield of hay in pounds per acre: Fairway	Yield of hay in pounds per acre: Standard
1 year old stands (av. of 6 tests)	1929–1938	2710	2700
2 year old stands (av. of 4 tests)	1930–1938	2849	2565
3 year old stands (av. of 3 tests)	1931–1938	1971	1913
4 year old stands (av. of 3 tests)	1932–1936	1899	1948
5 year old stands (av. of 3 tests)	1933–1937	896	829
Average yield per acre for a total of 19 tests		2065	1991

While the average yield of hay, as shown in Table 1, is slightly higher for the Fairway variety, the difference is small. These data show clearly, however, that the Fairway variety, under these conditions, is quite the equal of the so-called standard or taller types of created wheat grass as far as yield of hay is concerned. In addition, an average of all available data shows that hay from the Fairway variety possesses approximately ten per cent more leaf than that produced by the standard types.

While the height of the Fairway variety is usually somewhat less than that of the standard types—a ten-year average for Fairway is 13.7 inches as compared with 15 inches for the standard types—this deficiency so far as yield of hay is concerned is more than offset by its superior tillering capacity and higher percentage of leaf.

In seed yield the standard types have been more productive than the Fairway. The average yield of seed for the standard types is 487 lb. per acre as compared to 394 lb. for the Fairway variety. However, in comparison with other grasses, even the Fairway variety is an excellent seed producer.

Since crested wheat grass is highly drought resistant, and is being used extensively in regrassing abandoned lands in the drier areas in western Canada as well as in farm rotations to add fibre to the soil, the amount of root fibre produced by the different types is of interest.

Table 2.—Average field of root fibre

Age of stand (in years)	Pounds of root fibre per acre (dry weight) in top six inches of soil	
	Fairway	Standard
1	2500.72	2681.27
2	4519.36	4365.70
3	5307.79	3909.54
6	7431.10	5929.17
Average (All tests)	4939.74	4221.42

The above data show that the Fairway variety is definitely superior to the standard types for the purpose of adding fibre to the soil. In addition, examination of the root systems has shown considerable damage to the roots of the standard sorts from root-rotting organisms, whereas it is only rarely that lesions have been observed on the roots of the Fairway variety in these tests.

An examination of a large number of stems of crested wheat grass for sawfly larvae during the past season revealed the fact that the relatively fine-stemmed Fairway variety was practically free from this pest, whereas numerous larvae were found in the relatively coarse stems of the standard type. This is the result of one season's observations only, but the difference was striking. It is a matter of considerable importance that a perennial grass which, in many cases, is grown adjacent to fields of wheat be of such a nature that it will not act as a breeding ground for the wheat-stem sawfly.

From the data obtained to date, it is clear that the Fairway variety is at least the equal of the standard types in yield of hay. It is superior in the production of root fibre and leafiness as well as in rapidity of tillering and turf formation. Further investigation will be necessary in order to evaluate these types as regards the control of the wheat-stem sawfly. The Fairway variety is recommended for production throughout the dry-land areas of western Canada.

References

1. Bittera, N. v. Eine neue Pflanze für Wiesen und Weiden in trockenen Lagen. [A new plant for meadows and pastures in dry localities.] *Wien. landw. Ztg.* 87. 407. 1937. [*Agropyron cristatum.*]

2. BITTERA, N. v., and GRUBER, F. A taréjos búza és a magyar rossnok jelentösége száraz jelegü talajainkon, különös tekintettel gyökérfejlödésükre. [The importance of *Agropyron cristatum* and *Bromus inermis* in arid regions, with special reference to root growth.] Magyaróvár 1938. pp. 49. [German summary, 3-5.]
3. CANADA, Department of Agriculture. Pamphlet No. 157. N. S. Crested wheat grass. *By L. E. Kirk, T. M. Stevenson and S. E. Clarke.* 1934. pp. 22.
4. — ——————————— Publ. No. 557. Farmers' Bull. No. 28. Seeding crested wheat grass for hay and pasture. *By T. M. Stevenson, S. E. Clarke and F. M. MacIsaac.* 1937. pp. 14.
5. FAVORSKIĬ, N. V. [The reduction division in hybrids from *Secale cereale* × *Agropyron cristatum* (L.) Gaertn. with reference to their sterility.] *Social Zern. Hoz.* 1935. No. 1. 115-25. [English summary, 124-5.]
6. GRUBER, F. A szárazjellegü gyepes terület új füve : *Agropyron cristatum.* [A new grass for dry swards : *Agropyron cristatum.*] *Cukorrépa.* 11. 40-3. 58-9. Magyaróvár 1938.
7. HAY, W. D. Identification of Standard and Fairway strains of crested wheatgrass. *J. Amer. Soc. Agron.* 31. 620-4. 1939.
8. JOURNAL OF THE COUNCIL FOR SCIENTIFIC AND INDUSTRIAL RESEARCH. New grasses. *J. Coun. Sci. Ind. Res.* 5. 67. 1932. [Crested wheat grass, introduced from Canada, is being tested by the Division of Plant Industry, Australian Council for Scientific and Industrial Research.]
9. JUNATOV, A. A. [Natural seed sources of *Agropyron cristatum.*] *Selek. Semenovod.* 1935. No. 2/10. 63-4.
10. KAMINSKIĬ, A. E., and SCHNEERSON, V. M. [The place of *Agropyron cristatum* in the rotation] *Social. Zern. Hoz.* 1934. No. 4. 60-2.
11. KOSAREV, M. G. [Seed production of *Agropyron cristatum.*] *Selek. Semenovod.* 1935. No. 2/10. 59-62.
12. KRASNJUK, A. A. [*Secale cereale* × *Agropyron cristatum* hybrids.] *Social. Zern. Hoz.* 1935. No. 1. 106-14. [English summary, 113-4.]
13. KUZNECOV, V. A. [*Agropyron* (*A. cristatum, A. desertorum* and *A. sibiricum.*)] *Rastenievodstvo SSSR.* (*Plant Ind. U.S.S.R.*) 1. 519-26. 1933.
14. LOVE, L. D., and HANSON, H. C. Life history and habits of crested wheatgrass. *J. agric. Res.* 45. 371-83. 1932.
15. MONTANA Agricultural Experiment Station. Bull. No. 323. Crested wheatgrass in Montana. Comparisons with slender wheatgrass and brome grass. *By. L. P. Reitz, M.A. Bell and H. E. Tower.* 1936. pp. 53. [*Agropyron cristatum, A. tenerum* and *Bromus inermis.*]
16. PIPER, C. V. An unusual type of proliferation in *Agropyron cristatum.* *J. Hered.* 12. 423. 1921.
17. RHODESIA AGRICULTURAL JOURNAL. Crested wheat grass (*Agropyron cristatum.*) *Rhod. agric. J.* 31. 701-2. 1934.
18. SASKATCHEWAN University, College of Agriculture, Agricultural Extension. Bull. No. 54. Crested wheat grass. 1932. pp. 22.
19. STEVENSON, T. M., and WHITE, W. J. Growing crested wheat grass for seed production. 1935. pp. 9.
20. SURÁNYI, J. Adatok a taréjos buzafüröl. [Information on *Agropyron cristatum.*] *Köstelek.* 48. 353-4. 1938.
21. U.S. Department of Agriculture. Tech. Bull. No. 307. Crested wheatgrass as compared with bromegrass, slender wheatgrass, and other hay and pasture crops for the Northern Great Plains. *By H. L. Westover and others.* 1932. pp. 35.
22. ——————— ——————— Leaflet No. 104. Crested wheatgrass. *By H. L. Westover.* 1934. pp. 8.
23. VUKOLOV, V. Aklimatisace pýru hřebenitého u nás. [Acclimatization of *Agropyron cristatum* P.B. in Czechoslovakia.] *Čsl. Zeměd.* 18. 279. 1936.

REVIEWS

INTERNATIONAL LUCERNE TEST

Reviewer: G. M. Roseveare

The aims of the International Lucerne Test organized by the Imperial Bureau of Pastures and Forage Crops are outlined by R. O. Whyte in *Herb. Rev.* 1. 125-31. 1933. The test was laid down in that year at fourteen stations situated in twelve different countries. The Anstalt für Pflanzenbau und Pflanzenzucht [Institute for Crop Production] of the University of Jena, one of the two German Stations concerned, has now published through Dr. H. Bleier, in *Forschungsdienst*, 8. 153-72. 1939, a full report of the results obtained from 1933 to 1938.

The Jena trial has been conducted on the Station's experiment fields at Zwätzen, situated in the valley of the river Saale at an altitude of 145 m. The soil is medium to heavy loess loam, deep-bottomed, with a slight admixture of shell lime detritus, pH 7.1. Mean temperature (average of ten years) 90°C., mean rainfall 536 mm., mean duration of sunshine, March to October, 1,147 hours. The material for testing comprised four central Asiatic types, namely, Khivian, Semiryechensk, Turkmen and Middle Turkestan, and also the following: Asia Minor, Hungarian, Provence, Thuringian (a German hybrid lucerne), Grimm, and a hybrid type described as *Medicago falcata*. The material was sown down in five-fold replication on May 10, 1933, in plots of 11 sq. m. There were fifty-three plants to each plot, planting distance being 70 × 30 cm. The lucerne came up on May 19. Two or three cuts have been taken each year, when the plants were beginning to flower, and green weight, hay yield and protein content have been determined.

In addition to the above-mentioned plots, a second series of plants, 138 of each variety, was sown down 75 × 75 cm. apart for the study of seed yield and of morphological and other characters. Each year, with the exception of 1936, the first cut of this series was devoted to seed, harvested plant by plant. In 1936, the first cut was mown at flowering, plant by plant, the individual plant weight and ratio of leaf to stem were determined, and the second cut was grown on for seed.

The report gives full information on the findings at Jena in regard to weather; flower colour; the date at which flowering began, first and second cuts, 1934-38; ratio of stem to leaf; yield of green weight and hay, percentage of dry matter and crude protein, first, second and third cuts and total hay yield, 1933-38; grouping of plants within the different varieties in accordance with green weight yield, 1934, and yield of dry matter, 1936; longevity (number of plants within the varieties), 1933 to 1936 and 1938; chemical analysis, first and second cut, 1937, and of stems, leaves and inflorescences, and total plant, first and second cut, 1938; and seed yield.

At Jena, as in nearly all other trials of this nature, the superiority of the indigenous type—in the present case the Thuringian lucerne—has been clearly demonstrated. (Thuringian lucerne has been described by Klapp and Schubart in *Pflanzenbau*. 7. 353-65. 1931; see *Herb. Abstr.* 1. 90-1. 1931.) Thuringian took the first place for hay and seed yield, and was, moreover, the earliest variety to ripen. In proportion of leaf to stem, however, it took a middle position only, and it is suggested that the protein yield of this type might be improved by breeding for a higher proportion of leaf. Its early ripening may be of importance in the control

of the lucerne gall midge; experiments in this connexion have been set on foot. Although Thuringian compared rather badly with the other varieties in the character longevity, it led the way for yield in the first three years of the trial, together with *Medicago falcata* and the Hungarian and Asia Minor types. The taking of green cuts every year, without allowing the plant to ripen seed in the meantime, cannot be borne by Thuringian lucerne for longer than three years. This holds good for all the other varieties also, with the exception of Semiryechensk, Khivian and Middle Turkestan, in which the detrimental effects are felt still earlier.

Medicago falcata, the hybrid type, was found to be very similar to the Thuringian lucerne, although not quite so valuable.

The Hungarian, Asia Minor and Provence varieties are considered to be fairly good in yield characters, but are found poor in some other characters. The Asia Minor type, for example, is the least leafy.

Grimm exhibited remarkably little persistence at Jena and therefore played a poor part as regards hay yield, although in the first year of the trial it had a large number of plants of heavy weight. Its seed yield, however, was very good, and it was the most leafy variety.

The types from central Asia, namely, Semiryechensk, Turkmen, Khivian and Middle Turkestan, form a group of fairly similar constitution. In nearly every character they are the poorest of the types tested. An exception is presented in the longevity of the Turkmen type, which for this reason took the third place for yield in the last harvest year. Apart from perhaps this one character, the Asiatic lucernes do not appear to contain any more valuable hereditary characters than the German indigenous hybrid lucernes.

A full translation of the report will be published by the Bureau in the final report of the International Test of Geographical Types of Lucerne.

PASTURE CONTROL

[Reviewer: G. M. Roseveare]

On the Continent great importance is attached to the evaluation and recording of pasture productivity on the farm, as distinct from the study of pasture productivity in purely experimental work. This evaluation and recording is known as "pasture control." Although of relatively recent introduction, the value of such control, for the study of pasture economics and pasture management alike, has been amply demonstrated, both for the individual farm and for whole countries. That it is of importance for the farmer to know not only what yield he obtains from his arable land, but also the exact amount of hay and animal products (live weight, milk, etc.) produced by his grasslands, is obvious. Often he has no definite knowledge on this point, but relies either upon superficial observation or upon half-records, such as records of milk production only. Without definite records he has no means of knowing, for example, how much herbage goes to waste or provides mere "luxury feed" for animals. Where, however, the farmer has taken steps to measure the exact productivity of his grassland, without exception he has been enabled to reorganize his farm upon a more profitable basis. This reorganization has often entailed assigning a larger proportion of his land to temporary leys, sometimes the reduction of the permanent grassland area, and frequently the division of pastures into

paddocks. The German and Swiss farmers' journals contain many interesting accounts of reorganization of this type, carried out under widely varied environmental conditions (**13, 24** to **27, 34, 37**). But not only for the individual farmer are such records of value. Where available on a sufficiently comprehensive scale, they furnish the best possible basis for the study of grassland policy in any given region or country. As examples merely of studies of this nature there are cited articles by Elofson and his collaborators in Sweden (**5** to **10**), Sakshaug in Norway (**31, 32**), Charpentier in Finland (**2, 3, 4**), and Grandjean in Switzerland (**21, 21a**). Remarkably comprehensive studies of German grasslands by Geith have been made possible through the collection at Leipzig of a very large number of records from all parts of the country (**17, 19, 20**). It is noted by Geith that in 95 per cent of the pastures on which yield has been computed and recorded year by year, this practice in due course has been effective in securing yields considerably greater than the general average for the country (**19**). Elofson says : " I should like to emphasize how extremely desirable it is to control as many pasture farms as possible. Only when there are a large number of controlled farms is it possible for provinces and countries to judge the economic value of pastures and to educate the farmers accordingly " (**11**).

To record the yield of grassland, it must be possible to reduce all the products concerned—green cut, hay, maintenance feed, live weight increase, milk production, fat content of milk, etc.—to one common denominator. In Scandinavia this is the fodder unit (foderenhet) (**10**), in Germany it is the starch equivalent (**12, 14** to **16**). The two norms are interchangeable, for one fodder unit is equal to 0.7 kg. starch equivalent, and conversely 1 kg. starch equivalent is equal to 1.43 fodder unit (**18**). The German method of computing pasture yield, evolved by Falke and others, has already been described in this journal (**22**). The scale of values employed is as follows :

	starch equivalents kg.
Maintenance feed :	
cattle and cows weighing 200 to 400 kg.	0.65
,, ,, ,, ,, 400 to 600 kg.	0.55
,, ,, ,, ,, over 600 kg.	0.45
dry cows	0.55
foals, and horses on light work	1.—
horses on medium heavy work	1.20
Milk production :	
per kg. with up to 3 per cent fat content	0.24
,, ,, ,, 3 to 3.5 per cent ,, ,,	0.26
,, ,, ,, 3.5 to 4 per cent ,, ,,	0.28
,, ,, ,, over 4 per cent ,, ,,	0.30
Live weight increase :	
per kg., for animal of up to 500 kg.	2.5
,, ,, ,, ,, over 500 kg.	3.5
Calf birth	75.—

The scales of values in Scandinavia and Switzerland resemble the above, although differing slightly in some items (**18**).

The norms hitherto employed have been found to give, on the whole and for general purposes, a relatively reliable picture of productivity, but some degree of dissatisfaction with their lack of uniformity led the Third International Grassland

Congress at Zürich in 1934 to appoint a Committee to study them (**16**). The Committee, which was comprised of Dr. Elofson, Sweden, the late Dr. Wiegner and subsequently Dr. Grandjean, Switzerland, and Dr. Geith, Germany, reported to the Fourth Grassland Congress at Aberystwyth in 1937 that no uniform system had yet been evolved, although certain modifications and improvements had been made. These were enumerated (**18**). Dr. Elofson's opinion was that " the norms employed must be as simple and uniform as possible, as otherwise calculations will be too difficult and the results obtained by practical farmers too unreliable. The norms now presented have been so thoroughly tested by grassland farmers and stock raisers, and are based upon such wide experience, that any material alteration is hardly expedient. Improvements, naturally, must always be sought, and any contribution in this direction is welcome. In particular, we are anxious to learn the experience of overseas countries " (**11**).

The proposal of a simpler norm now comes from Prof. Richardsen, Berlin and Hamburg, himself a pioneer of the grassland control system (**28**). He notes the desirability of inducing as many farmers as possible to record the productivity of their grasslands, but considers that the starch equivalent conveys little meaning to them, and in addition makes calculation difficult. The substitution of a norm called the " grassland performance unit " (Grünlandleistungseinheit) is proposed (**29**). The German abbreviation is G.L.E. ; the equivalent English abbreviation G.P.U. The scale of values given is as follows : 1 grassland performance unit = 1 kg. live weight increase = 24 hours' maintenance feed for one head of cattle = 10 kg. milk = feed for 1 working day, horse or ox = one-quarter dz.* green weight = one-twelfth dz. hay. The values for milk, hay, etc., can be modified in accordance with quality. The greater simplicity of the G.P.U. in use is illustrated by the following comparison, in which first the starch equivalent and then the grassland performance unit is taken as the norm.

(a)

				Starch equivalents
789 kg. live weight increase	=	789 × 2.5	=	1,972.5
935 cattle pasture days†	=	935 × 2.5	=	2,337.5
8,574 kg. milk	=	8,574 × 0.25	=	2,143.5
		Total productivity :		6,453.5 starch equivalents

(b)

				G.P.U.
789 kg. live weight increase	=	789 × 1	=	789
935 cattle pasture days	=	935 × 1	=	935
8,574 kg. milk	=	8,574 ÷ 10	=	857
		Total productivity :		2,581 G.P.U.

The proposal is further elucidated in a subsequent article (**30**). It is claimed that the G.P.U. is simpler not only for the farmer, but also for purposes of international comparison. It can be reduced to starch equivalents if desired, for 1 G.P.U. = 2.5 starch equivalents.

*1 dz. = 100 kg.

†1 cattle pasture day = maintenance feed for 500 kg. live weight for twenty-four hours.

Whereas Richardsen objects to the present norms as too complicated for the farmer to use, Prof. Woehlbier, in a recent article, considers the starch equivalent inadequate for judging the exact quantity of herbage consumed by the animal, its digestibility, the extent to which it is utilized, and whether or not there is a wastage of valuable nutrients such as, for example, protein. He outlines a method evolved by him at the Agricultural College, Hohenheim, near Stuttgart, whereby a parallel experiment is conducted with two groups of animals, one group being fed in the stall on herbage from the pasture in which the second group grazes free. For the stall-fed group coefficients of digestibility are determined ; for the second group merely the quantity of excreta, and by means of the already ascertained digestibility coefficients the quantity of herbage absorbed can be determined. It would appear, however, that Woehlbier's method is designed rather for the experimentalist than for the farmer or the worker surveying regional productivity (**36**).

In the English-speaking countries the evaluation of grassland productivity has received little attention until quite recently. At the final meeting of the Fourth International Grassland Congress in Great Britain, 1937, a resolution was passed to set up working committees to determine the nutritional value and relative costs of grassland crops in comparison with other crops, particularly in the English-speaking countries. A record of progress to date is presented by Whyte in a previous part of this journal (**35**). Work of an exploratory nature has been published by Schuster in 1929 and more recently by Ahlgren, Bohstedt and Aamodt in the United States (**33, 1**), and Hinman, Cornell University, notes the value of live weight gains as a measure of pasture yield (**23**).

Literature

1. AHLGREN, H. L., BOHSTEDT, G., and AAMODT, O. S. Problems in evaluating pastures in relation to other crops. *J. Amer. Soc. Agron.* 30. 1020-9. 1938. *Herb. Abstr.* 9. Abs. 385. 1939.
2. CHARPENTIER, C. A. G. Pastures and pasture experimental work in Finland. *Herb. Rev.* 1. 83-5. 1933.
3. ——————— Viljelyslaitumen perustamista ja hyväksikäyttöä koskevia tutkimuksia Vv. 1927-1936. Investigations concerning the preparation and utilization of cultivated pastures during 1927-1936. *Valt. Maatalousk. Julk.* 88. 1-163. [English summary, 147-63.] 1937. *Herb. Abstr.* 7. 288-9. 1937.
4. ——————— Redogörelse för de senaste årens erfarenheter rörande produktionskostnaderna för foder och animaliska produkter vid betesgång. Kort redogörelse från Finland. [Report on recent experience concerning the cost of production of herbage and animal products on pasture. Short report from Finland.] *Beretn. Nord. JordbrForskn.* 6. *Kong. Uppsala.* 1938. 396-404.
5. ELOFSON, A., and WALLIN, B. De svenska betesmarkernas avkastning. [Yield of Swedish pastures.] *Kungl. Landtbr. Akad. Handl.* 69. 68-103. 1930.
6. —— ———————, and NANNESON, L. Svenska Betes- och Vallföreningens kontrollgårdar. [Control farms of the Swedish Grassland Association.] *Svenska Betes- o. Vallfören. Årsskr.* 15. 20-52. [German summary, 50-1.] 1933.
7. ——————————— Gårdskontrollen vid Blombacka och Boda. [Farm control at Blombacka and Boda.] *Medd. svensk. Betes- o. Vallfören.* 1. 1-87. [German summary, 84-7.] 1933. *Herb. Abstr.* 4. 126. 1934.
8. ——————————— Gårdskontrollen vid Blombacka och Boda. II. [Farm control at Blombacka and Boda. II.] *Medd. svensk. Betes- o. Vallfören.* 4. 1-66. [German summary, 62-6.] 1934. *Herb. Abstr.* 6. 76-7. 1936.

9. Elofson, A., and Wallin, B. Kontrollgårdarna. [The control farms.] *Svenska Betes- o. Vallfören. Årsskr.* 16. 38-59. 1934.

10. ——— Normer för beräkning av betesmarkernas avkastning. [Norms for the calculation of pasture yield.] Foreword by A. Elofson. *Svenska Betes- o. Vallfören. Årsskr.* 17. 191-201. 1935.

11. ——— *Rep. Fourth Int. Grassl. Cong.* 1937. p. 440.

12. Falke, F. Die Ertragsermittlung im Weidebetriebe und die vom Sonderausschuss der Deutschen Landwirtschafts-Gesellschaft für Wiesen und Dauerweiden aufgestellte Berechnungsweise. [The determination of yield in pasture farming, and the method of calculation evolved by the German Agricultural Association's special Grassland Committee.] *Verh. 1. Tag. Weide- u. Wiesenwirte.* [*Rep. First. Int. Grassl. Cong.*] Berlin, 1929. 77-110.

13. Friederichsen, W. Die Ernährung des Rindviehs auf wirtschaftseigener Grundlage mit besonderer Berücksichtigung der Verhältnisse an der Ostküste Schleswig-Holsteins. [The home production of cattle fodder, with special reference to the east coast of Schleswig-Holstein.] *Jb. Erfahr. Weidew.* 12. 18-24. 1936. *Herb. Abstr.* 7. 345. 1937.

14. Geith, R., and Fuchs, K. Grünlandfibel. [Grassland primer.] 2nd edn. Arb. Reichsnährstandes. 13. Berlin, 1936. pp. 80. *Herb. Abstr.* 7. 279. 1937.

15. ——— Die Weideertragsermittlung in Deutschland. [Determination of pasture yield in Germany.] *Verh. 2. Tag. Weide- u. Wiesenwirte.* [*Rep. Second Int. Grassl. Cong.*] 1933. 134-40. [English summary, 139-40.]

16. ——— Neuere Untersuchungen zur Weideertragsermittlung. [Recent investigations on the determination of pasture yield.] *Rep. Third Int. Grassl. Cong.* 1934. 427-36. [English summary, 434.] *Herb. Abstr.* 5. 31. 1935.

17. ——— Weideerträge und Weidebetrieb. [Pasture yields and pasture management.] *Mitt. Landw.* 50. 611-2. 1935. *Herb. Abstr.* 5. 218. 1935.

18. ——— Die Verbesserung der Normen zur Ermittelung des tierischen Nutzertrages einer Weide. The improvement of the norms used for the determination of a pasture's yield of animal products. *Rep. Fourth Int. Grassl. Cong.* 1937. pp. 434-40. [English summary, 438.]

19. ——— Die Leistung der deutschen Weiden und Wege zu ihrer Verbesserung. [The performance of the German pastures and ways of improving it.] *Forschungsdienst.* Suppl. 8. 63-8. 1938. *Herb. Abstr.* 8. Abs. 1094. 1938.

20. ———, and Zuern, F. Die Leistungsfähigkeit der Dauerweiden und der Einfluss des Alters der Weide auf den Ertrag. [The productivity of permanent pastures and the influence of age upon yield.] *Futterb. GärfBereitg.* 1938. No. 3. 161-8. *Herb. Abstr.* 8. Abs. 1091. 1938.

21. Grandjean, S. Die Ertragsermittlung der Weide. [Determination of pasture yield.] *Mitt. Lebensm. Hyg. Bern.* 24. 1. 1933.

21a. ——— Untersuchungen über Pflanzenertrag und tierischen Nutzertrag einer durch Milchvieh genutzten Talweide. [Investigations on plant yield and utilization by animals of a valley pasture stocked with milch cows.] *Schweiz. Landw. Mhft.* 1933. pp. 27. *Herb. Abstr.* 4. 24. 1934.

22. Herbage Reviews. The German system of calculating pasture yield. *Herb. Rev* 1. 112-3 and 5 sample pages. 1933.

23. Hinman, R. B. Live weight gains as a measure of pasture yields. *Proc. Amer. Soc. An. Prod.* 1937. 83-4. *Herb. Abstr.* 8. Abs. 1093. 1938.

24. Kauter, A. Ertragsermittlungen auf Jungviehalpen. [Determination of productivity on alpine grazings for young cattle.] *Schweiz. landw. Mh.* 17. No. 2. 1939. pp. 10. *Herb. Abstr.* 9. Abs. 1295. 1939.

25. Kloeppel, R. Bericht über mehrjährige Weideertragsermittlungen im Ostpreussen. [Report on several years' determination of pasture productivity in East Prussia.] *Z. PflErnähr. Düng.* 40. 200-14. 1935. *Herb. Abstr.* 6. 44. 1936.
26. Koch, G. Die Erzeugung und Verwertung wirtschaftseigenen Futters in einem bäuerlichen Betrieb. [The home production of fodder on a small farm and its value.] *Jb. Erfahr. Weidew.* 12. 25-33. 1936. *Herb. Abstr.* 7. 345. 1937.
27. Kunack, Meine Erfahrungen bei der Umstellung meines Betriebes auf Weide und wirtschaftseigene Eiweissversorgung. [Reorganization of a farm for pasture and the home production of protein.] *Jb. Erfahr. Weidew.* 12. 7-17. 1936. *Herb. Abstr.* 7. 344-5. 1937.
28. Richardsen. Notwendigkeit und Durchführung einer planmässigen Weidekontrolle; fünfjährige Ergebnisse auf besten alten Marschweiden in Nordfriesland. [Necessity for systematic pasture control and its organization; five years' results on best quality old marshland pastures in North Friesland.] *Jb. Erfahr. Weidew.* 2. 91-100. 1914.
29. ——— Das Einfachverfahren zur planmässigen Grünlandkontrolle. [The simplified method of systematic grassland control.] *Mitt. Landw.* 53. 467. 1938. *Herb. Abstr.* 8. Abs. 1092. 1938.
30. ——— Das Einfachverfahren zur planmässigen Grünlandkontrolle. II. [The simplified method of systematic grassland control. II.] *Mitt. Landw.* 54. 550-1. 1939. *Herb. Abstr.* 9. Abs. 1296. 1939.
31. Sakshaug, B. Beitekontroll på Ekset i Volda. [Controlled grazing at Ekset in Volda (Norway).] *Årb. Beitebr. Norge.* 13. 5-11. 1938. *Herb. Abstr.* 9. Abs. 413. 1939.
32. ——— Produktionskostnaden for beitegras. Norske undersøkelser og erfaringer fra de senere år. [Cost of production of pasture grass. Norwegian investigations and experiences in recent years.] *Beretn. Nord. JordbrForskn.* 6 *Kong. Uppsala.* 1938. pp. 405-11.
33. Schuster, G. L. Methods of research in pasture investigations. *J. Amer. Soc. Agron.* 21. 666-73. 1929.
34. Voedisch, G. Ein richtiger Wirtschaftsaufbau, die Grundlage für die Steigerung der wirtschaftseigenen Futtererzeugung. [Correct farm organization the foundation of increased home fodder production.] *Mitt. Landw.* 51. 826-7. 1936.
35. Whyte, R. O. The comparative nutritive value and relative cost of forage (pasture and hay) and other crops. *Herb. Rev.* 7. 24-6. 1939.
36. Woehlbier, W. Grundsätzliche Betrachtungen zur Frage des Weideertrages. [Observations on the problem of pasture yield.] *Forschungsdienst.* 7. 260-4. 1939. *Herb. Abstr.* 9. Abs. 519. 1939.
37. Zuern, F. Warum neuzeitliche Weidewirtschaft? [Reasons for modern pasture management.] *Weidew. Futterbau Beil. dtsch. landw. Tierz.* 12. 25-6. 1937. [An economic study of results obtained on five farms.]

A GRASSLAND SURVEY OF THE FALKLAND ISLANDS

[Reviewer: R. O. Whyte]

In the period between November 20, 1937, and March 11, 1938, W. Davies made a comprehensive survey of the Falkland Islands in order to study the present position of the grasslands and to make recommendations for their improvement. The observations made during this tour are published in a special report, entitled " The

grasslands of the Falkland Islands " (Government Printer, Stanley, Falkland Islands ; Crown Agents for the Colonies, 4 Millbank, London, S.W.1, 1939, pp. 96. pls. maps, price 5s.).

The Falkland Islands lie in the South Atlantic Ocean some 300 to 400 miles east of the southern extremity of South America, in about the same latitude (south) as that part of Wales south of Aberystwyth. The aggregate area of the small archipelago (two main islands and a large number of adjacent islands) is about three million acres, and the population about 2,500, of whom more than half live in the only town, Stanley.

According to records taken at Cape Pembroke (near Stanley), the Falkland summer is considerably cooler than that of southern Britain, but the average winter temperatures are not much below those of the British stations quoted in Table 1.

The monthly mean temperatures for January and July at Cape Pembroke (Stanley), Kew, and Aberystwyth

Cape Pembroke (Stanley)		Kew (40 years' normal)		Aberystwyth (1919-27 average)	
	Fahr.		Fahr.		Fahr.
Jan. (summer)	49.3°	July (summer)	62.7°	July (summer)	59.3°
July (winter)	36.7°	Jan. (winter)	38.8°	Jan. (winter)	43.2°

The average rainfall at Cape Pembroke is about 25 in., fairly evenly distributed throughout the year. Excessive rainfall is uncommon, and there are about 250 rainy days in the year. Snow does not lie for long periods in the lowlands. The chief characteristic of the Falkland climate is its extreme variability over any 24 hr. period, and the persistency of the wind. Rainfall in the uplands is much higher than in the lowlands ; it is considered probable that, climatically, the uplands stand in much the same relationship to the country at lower elevations as do the British uplands to British lowlands.

Sheep are the most numerous of the livestock ; the highest number was carried in 1898 (about 807,000), but there has subsequently been a more or less gradual decline to the present figures of about 600,000. Figures indicate that there has been a considerable fall in gross wool production, and in the average annual wool clip for sheep. Other livestock include 3,500 horses and 9,500 cattle, the latter being used as foragers on the sheep stations with the aim of maintaining the pastures in better condition for sheep. Dairying is in a primitive state of development, imported dairy produce being widely used.

The sheep stations are commonly over 100,000 acres, and wool is the chief export. The present carrying capacity is about one sheep to five acres. Individual paddocks or fields are frequently more than 10,000 acres in size. A few good pastures have been formed as a result of special sowings, in which wild white clover has played an important part. Apart from these leys, dense swards of bent (*Agrostis* spp.) have been formed by intensive grazing in some of the settlement fields ; these carry more than a sheep to the acre.

W. Davies summarizes his conclusions as follows :

" The general grassland problems of the Falkland Islands have been considered with particular reference to the possibilities of improving the herbage and consequently the stock-maintaining capacity of those grasslands. There can be little doubt that many of the natural grazings of the colony are amenable to improvement. The general indications are that such improvements are likely to be best brought about by a substitution of the present species by more suitable introduced plants.

There are no native legumes of any kind belonging to the Falklands, but a number of European legumes appear to thrive if once properly established. Notable among these is white clover. Wild white clover may be regarded as the fundamental plant in any scheme of grassland improvement contemplated in the Falklands, indeed, it has been shown to play this role over a very wide area of world grasslands in temperate regions. If white clover is the key species, it remains for Falkland Islanders themselves to find the proper means of introducing and establishing this clover all over their stations, and having regard to local conditions and the economic life of the colony in general.

" There is a large number of grasses and grass-like plants (these latter not in the family Gramineae) native to the Falkland Islands. Some of these are very valuable—such as, for example, the native tussac (*Poa flabellata*). Taking the native grasses as a whole, however, they are of low nutritive value when compared with British grasses grown on the same soil. The case again is formulated in favour of specifically introducing new grasses to replace wherever possible the existing native flora. Many grasses and herbs of British origin are known to flourish under certain conditions in the Falklands. Of immediate interest in this respect the following plants may be quoted : Yorkshire fog, red fescue, timothy, cocksfoot, ribgrass, and yarrow. Experience may show that there are others that are worth while cultivating, and particularly may this be true of a number of clovers and other legumes.

" The present system of grassland farming in the Falkland Islands is nothing short of large-scale ranching. Until a methodical and much extended scheme of subdividing existing paddocks is brought about, the potentialities for land improvement throughout the colony will remain all but untapped. There is no doubt at all that closer subdivision with the creation of smaller fields on which a practical form of rotational grazing can be employed is fundamental to pasture improvement. Indeed, it may well be said that a well conceived programme of subdivision is essential to the pastoral industry. The fall in the stock-carrying capacity of the pastures and, therefore, in the pastoral wealth of the colony, has been remarked upon. The decline is still proceeding and there can be no doubt that deterioration in the grasslands themselves is taking place and is, indeed, the cause of the decline in production. As regards the Falklands, all the evidence suggests that pasture deterioration will take place progressively the more rapidly in proportion as the stock carried becomes less. The hope of the industry lies in increased production and in carrying an ever-increasing head of stock. (This is said with the knowledge that many owners and others connected with the Falklands take the converse view.) Increased production means that pastures will have to be improved, and properly maintained improvements of pastures will only be possible after first creating smaller fields and introducing better methods of grazing management.

" The time has arrived when the Falklands must consider very seriously whether the present ranching policy is to continue, or whether a complete change of methods involving a policy of grassland improvement together with a more intensive system of pastoral agriculture is to be put into effect. Continuance of the existing ranching system cannot but lead to a still greater lowering of carrying capacity, and to the decreased wealth of the country as a whole. With a change over in methods and the gradual substitution of a more intensive type of grassland farming the decline in production would cease, and after a time there is no reason why definite and progressive increases should not be recorded. Subdivision of paddocks, the better management of pastures, and the replacement of the present herbage by better plants are all essentials in the developmental scheme.

" In a short, but entirely interesting, reconnaissance survey of the kind described in the foregoing report, no more than general indications can be given. Similarly

only broad generalizations can properly be made. The sequel to such a reconnaissance should be the setting in motion of properly planned machinery throughly to investigate the broad issues that have been raised. It is submitted, therefore, that investigational work dealing specifically with the grassland problems of the Falkland sheep stations should be conducted. Such investigational work would be carried out in the colony under the general supervision of the Director of Agriculture. Specific problems connected with the practical, rather than the purely scientific, aspects of grassland development would obviously take precedence in any such research scheme."

Certain miscellaneous points touched upon in the Report may be of some general interest, and will be referred to briefly in this review.

The climax vegetation is grassland. The most abundant indigenous species is *Cortaderia pilosa* (white grass). Introduced grasses such as *Agrostis* spp. and *Poa pratensis* are important in closely-grazed settlement pastures. Another herbage plant of local importance is *Juncus scheuchzerioides*.

Special sections of the Report are devoted to pasture improvement on fields around the settlements, seeds mixtures for these fields and for the open camp grassland, the merits of rotational grazing, fencing and sub-division of paddocks, burning for grassland improvement, legumes and soil fertility, inoculation of white clover sowings, and the value of certain weeds in land improvement. The example of the value of *Plantago* spp. and other weeds in British grasslands is used to support a claim for the study of weed species in the Falklands in order to provide a more balanced ration than is now available.

The possibilities of seed production of the necessary herbage plants in the Falklands is discussed ; in connexion with the production of white clover seed, the introduction of bees is considered to be advisable and feasible.

A special note was made of the penguin grounds ; these show that, where excessive quantities of nitrogen-rich residues are applied to the surface soil in the form of penguin excreta, the mat so characteristic of Falkland pastures breaks up and a soil of higher fertility is produced. It is therefore necessary to narrow down the carbon : nitrogen ratio, either by the application of nitrogenous fertilizers (uneconomic in the Islands), or by the introduction of a nitrogen-enriching plant, that is, white clover or other legumes.

W. Davies considers that the tussac grass of the Falklands (*Poa flabellata*) appears to have all the valuable characters of a specialized crop for winter fodder. If grown in conditions of high soil fertility, it makes an abundance of leafy growth during the summer, and this remains wholly winter green. It appears to be able to withstand complete defoliation (cutting rather than grazing) in winter, but is apparently unable to resist continued defoliation during the summer. Horses and cattle are said not to harm the plant, but uncontrolled grazing with sheep will rapidly deplete areas of tussac. If this grass is to be grown as a forage crop, it will require high fertility, particularly available nitrogen, and freedom from competition of other plants.

Special mention is made of the reclamation of sand drifts and other denuded areas, wind erosion being an important problem in the Islands.

A supplementary report is published in the same volume, and deals with evidence based upon the chemical analyses of samples of grasses and other plants collected in the Falkland Islands, and analysed subsequently at Aberystwyth. The indigenous grasses are of low mineral content and of poor nutritive value ; many of the native miscellaneous herbs have a much higher mineral content. Eight species of pasture plants (three grasses, one clover, and four herbs common in Britain) showed on analysis a similar protein and mineral content, whether grown in the Falkland Islands or in Britain.

THE FODDER VALUE OF THE WILD FLORA OF MANCHOUKUO*

[Reviewer : R. O. WHYTE]

The Report of the Institute of Scientific Research, Tatsung Tachie, Hsinching, Manchoukuo, for April, 1939 (Vol. 3. No. 2. pp. 39-144), comprised an account of a study of the components of the natural flora in the vicinity of Hsinching, with special regard to their flowering period, yield, chemical composition, vitamin C content and general utility as fodder for animals. An abridged translation of parts of this report is given below. It may be noted that this study resembles some of those made in the Soviet Union, in which representatives of many plant Orders, other than the more generally recognized Gramineae and Leguminosae, are studied as to their fodder value.

Results of comprehensive research carried on for many years throughout the Soviet Union were embodied in 1937 in a book entitled, " Fodder plants of the natural grasslands of U.S.S.R." (in Russian). In this book some 3,000 species belonging to 116 families were dealt with separately from the fodder point of view, with the result that many of the plants studied were recommended, either for immediate use or for breeding purposes. In two articles in *Herb. Rev.* Vol. 5. No. 3. 1937, Professor I. V. Larin, Editor-in-Chief of the above-mentioned book which was issued by the Collegium of the U.S.S.R. Institute of Fodders, gave a general review of the contents of the book.

While such research does not apply to conditions where clover-grass or legume-grass pastures or meadows are easy to establish and maintain, the results of the Soviet research on the miscellaneous natural Orders and of this Japanese work will be of some interest in other conditions, where the rapid provision of a vegetative cover, both as a protection for soil and as a grazing resource is an important problem.

The flowering period of the plants studied varied from the middle of June to the end of September, but individual species differed widely, the duration of flowering ranging from 20 to 80 days. Those with the longest flowering periods were *Aster holophyllus*, *Amarantus retroflexus*, *Persicaria bungeana*, and *Setaria lutescens*. The length of the flowering period corresponds as a rule to that of the growing period, but some species do not necessarily follow this generalization. The plants were grouped under three heads according to their flowering periods : (1) those flowering before mid-summer, say, July 15, (2) those flowering during mid-summer, July 15 to August 15, and (3) those flowering after mid-summer, after August 15.

The yield of the species was measured by cutting areas approximately 6 ft. sq. in size ; those with poor yields gave less than 1,000 kg. per ten ares, while those with large yields exceeded 3,000 kg. The species examined were classified in four groups on a yield basis.

Poor yields

Poa pratensis	*Agrimonia pilosa* var. *viscidula*
Cirsium segetum	*Persicaria bungeana*
Aster holophyllus	*Lappula hetracantha*
Sonchus brachyotus	*Leonurus sibiricus*
Kummerowia stipulacea	

*From a translation made by B. Matsukawa from a paper by M. Saito, M. Watanabe and M. Kozima.

Medium yields

Aneurolepidium chinense	*Melilotus suaveolens*
Roegneria ciliaris	*Salsola collina*
Calamagrostis epigeios	*Geum aleppicum*
Setaria lutescens	*Persicaria lapathifolia*
Artemisia scoparia	*Persicaria cochinchinensis*
Erigeron canadensis	*Plantago asiatica*
Aster holophyllus	

Large yields

Setaria gigantea	*Xanthium japonicum*
Echinochloa villosa	*Amarantus retroflexus*
Cirsium setosum	*Abutilon Avicennae*
Persicaria nodosum	

Very large yields

Echinochloa Crus-galli ssp. *submutica*	*Chenopodium centrorubrum*
Artemisia venusta	*Cnidium Monnieri*
Artemisia selengensis	*Sphallerocarpus gracilis*

The vitamin C content was found to be more variable than the yield, the substance reduced from 1 grm. of fresh material varying from a minimum of 0.045 mg. to a maximum of 2.99 mg. In general, it may be said that the Gramineae and Compositae contain comparatively little vitamin; the Leguminosae are much superior in this respect and the Polygonaceae contain a considerable amount of the "reduced substance".

There was some variation in the palatability of species of the Gramineae to cows, horses, and sheep, but no plants of this Order were partially or totally unpalatable to the animals, as were some plants of other Orders. For instance, the palatability of Compositae varied greatly with horses, cows, and sheep. A particularly distinct preference was shown by these animals for the species *Cirsium setosum*, *C. segetum*, and *Artemisia selengensis*; the taste of horses on the one hand, and of cows and sheep on the other are, however, completely opposite. In other Orders, too, many species were suitable for cows and sheep, but not for horses. The authors studied each species carefully in this respect.

Chemical analyses were made of the thirty-six species, the percentage dry matter being first estimated. The Gramineae, Leguminosae and Rosaceae gave high dry matter yields, the figures being in the neighbourhood of 35 per cent, but percentages fell as low as 25 or thereabouts in plants of Compositae, Polygonaceae, Umbelliferae, etc.

The plants of the Gramineae were found to contain little protein and much fibre; the Compositae, on the other hand, much protein and little fibre, and their fat content was high compared with other Orders. The Leguminosae contained more protein than the Compositae; the Chenopodiaceae could equal the Leguminosae in this respect, or it may be said that the proteins in the former were more concentrated than in the latter. The Rosaceae were similar in this respect to the Gramineae and the Polygonaceae to the Compositae.

The phosphorus and calcium contents of the Gramineae were low; the Compositae were a little better, and the Leguminosae, Rosaceae, Umbelliferae and Polygonaceae were highest. A high phosphorus and calcium content was found in *Abutilon Avicennae* and *Amarantus retroflexus*.

The phosphorus/calcium ratio was also considered. The species studied were found to contain generally more calcium than phosphorus; in some cases a small ratio of 1 : 1 was found, but in others it was as much as 1 : 14. In the Gramineae the ratio of calcium was small (1 : 1 to 1 : 2); the Compositae had a higher ratio of

1 : 3 in many plants, although other species in this Order were rich in calcium, *Cirsium setosum* and *C. segetum*, having a ratio of more than 1 : 10. The calcium ratio was also as high as 1 : 5 or higher in other Orders, for instance, Chenopodiaceae, Rosaceae, Polygonaceae, Umbelliferae and Malvaceae.

In summarizing the facts obtained regarding the thirty-six natural species studied and in discussing them from a fodder point of view, the authors state that it must be remembered that the value of wild species as fodder cannot be determined by one or two single factors alone, as it depends upon varied complex conditions. Large yields, rich nutrient production and suitability for cattle feeding are certainly important factors, but, in addition, flowering time and duration, length of growing periods, time of lignification, etc., must also be taken into consideration. For instance, if the growing period of a wild species is prolonged, cattle may graze it for a long time, and lateness in flowering means that a supplementary nutrient may be expected late in the autumn when the supply of other wild species is declining, thus increasing the fodder value of the species in question. Further, a species which becomes lignified at an early stage of its growth is of limited value, no matter how large the yield may be, and conversely, a species which can remain tender for a lengthy period is of higher value even if its yield should be small. Taking these points into consideration, the authors procced to examine a few wild species, classifying them under the following three heads :

(a) Species of a higher value than hitherto appreciated,
(b) Those whose value has already been recognized and is now confirmed, and
(c) Those which may profitably be cultivated as fodder.

A. *Wild species formerly considered of little value, but no.v recommended for cultivation.*

(1) *Echinochloa Crus-galli* subsp. *submutica*

This grass gives the largest yield in the Gramineae, remains tender for a fairly long period and its growing period before flowering is long. It is of average nutritive value and is very palatable to cows, horses and sheep. The species is therefore useful both as grazing and as fodder.

(2) *Aster holophyllus.*

Yield is small, but the plants contain much nutrient, resembling the Leguminosae in this respect. Both the growing and flowering periods are long and plants remain tender even after flowering. The proportion of leaves is high. Being relished by cows, horses and sheep the species is of great value for grazing and fodder production.

(3) *Kummerowia stipulacea*

Yield again small, but plants rich in protein, nutrients and calcium. The leaves and stems are very tender and the growing period before flowering is comparatively long. A particular advantage of this species is that it flowers late in summer, thus providing fodder for autumn use; the species does not become lignified even after flowering. It is palatable to cows, horses and sheep and is useful for grazing and fodder production.

(4) *Sonchus brachyotus*

Yield not large, but protein content high ; probably the most nutritive of the Compositae. When green it contains much water, is very tender and does not lignify even after flowering. Palatable to cows, horses and sheep, and suitable for fodder.

(5) *Bidens parviflora*

Yield small, but rich in protein and nutrients. Flowering occurs early in autumn, thus providing autumn fodder. Succulence is retained for a fairly long period. Palatable to cows, horses and sheep, and suitable for both grazing and fodder production.

B. *Species whose value has already been recognized and is now confirmed.*

(1) *Aneurolepidum chinense*

Yield medium, but the species grows extensively in the high plains of Manchuria. It is highly cold resistant, and its growing period is long. Although not rich in nutrient, the plants are soft and do not lignify. They grow in colonies and are always palatable to cows, horses and sheep, thus being useful as fodder and for grazing.

(2) *Roegneria ciliaris*

Yield medium. Species similar to that just described, although it should be utilized earlier in the season.

(3) *Echinochloa villosa*

This species resembles others in a low protein content, but has special features in its large yield, fairly tender growth and large proportion of leaves. Growth particularly vigorous from late summer to early autumn.

C. *Species which may profitably be cultivated as fodder under special conditions,*

(1) *Chenopodium centrorubrum*

Exceedingly large yield, protein, calcium and vitamin C contents high, nutritive value equal or superior to the legumes. Deserves cultivation, and is palatable to cows and sheep, but not to horses. Stem lignifies considerably on flowering, and leaves lose their succulence and their value as fodder. Time of cutting is therefore important.

(2) *Cnidium monnieri*

Yield again large, nutritive value inferior to Chenopodiaceae but superior to Gramineae. Plant is tender and does not lignify, even after flowering. Not palatable to horses.

(3) *Amarantus retroflexus*

Yield large, protein, calcium and vitamin C contents high, equal to the Leguminosae. Succulent when young, but unfit for fodder when mature. Palatable only to sheep. It is therefore important to devise means of making it more acceptable as fodder.

(4) *Xanthium japonicum*

Yield rather more than medium. Protein content and nutritive value equivalent to the legumes. Succulent when young, but lignifies with advancing maturity, becoming worthless as fodder. Palatable to cows. Fruits possess sharp thorns, harmful to animals. Cultivation profitable only under special conditions, taking these mentioned defects into account.

(5) *Persicaria lapathifolia*

Yield medium, but less than other plants of the same Order. Bitter taste of related plants absent. Stem fairly tender, but becomes lignified if cutting is delayed. Rich in vitamin C, similar to Compositae in other nutrients. Unpalatable to cows and horses, but palatable to sheep. Can therefore be cultivated as fodder under special conditions.

(6) *Artemisia venusta* and *A. selengensis*

Both species have a very large yield. Nutritive value slightly superior to Gramineae, fairly tender. Their chief defect is unpalatability to cows and sheep, which particularly avoid their flowers. They are, however, palatable to horses and are considered worth cultivating under special conditions.

PHASIC DEVELOPMENT OF PLANTS (4)

A review recently prepared by the staff of the Imperial Bureau of Pastures and Forage Crops, and published under the authorship of R. O. Whyte, *Biol. Rev.* 14. 51-87. 1939, is being summarized and supplemented in serial form in successive issues of *Herbage Reviews*. The first discussions appeared in the March, June and September issues of this year, pp. 27-32, 94-9 and 181-9 respectively.

Physiological Phases of Development

We have so far described developmental phases in terms of those environmental factors which determine their inception and progress ; this is an ecological approach. It is possible to approach the same problem from another angle, namely, upon the basis of those internal readjustments which occur in plant tissues, and which, through a succession of morphological readjustments in the tissues, ultimately bring the plant organs to reproduction ; this is a physiological approach.

From this point of view, development appears as a single entire complex of physico-chemical reactions in which any two components, although in a strict sequence, cannot strictly speaking be separated from each other, and still less contrasted one with the other, as is in fact assumed in the conception of " the transition from the vegetative to the reproductive phase." A developmental phase is not something new and different, but a continuation of earlier physico-chemical reactions ; for their continuation, or for some of the concomitant reactions, however, different environmental conditions may be required. With this reservation we may indeed speak of physiological phases involving a number of related and congruous, but not necessarily conterminous physico-chemical reactions.

Protoplasm, the primary bearer of all vital reactions of plant tissues, changes continuously and in various ways. It is difficult to say when these changes " trespass the limits beyond which a quantity is converted into a quality" ; it is still more difficult, and certainly too presumptuous to identify these complex changes of protoplasm with particular "photo-chemical," "scoto-chemical," "thermo-chemical" and other reactions. Any attempt to simplify these extremely complex physico-chemical reactions in plant tissue as, for instance, by the C/N hypothesis, is *a priori* doomed to failure.

More particularly since the classic work of Klebs early in this century, protoplasm has been the subject of many physico-chemical studies, but we are nevertheless far from a full and detailed knowledge of the subject. This is due to the complexity and variability of the physico-chemical response of protoplasm to environmental factors. Moreover, the well-established physiological differentiation of morphologically indistinct parts along a stem (pp. 77-8 of the review) suggests that these physico-chemical reactions are localized in the meristematic cells, retained there and transmitted only through concurrent meresis ; this renders the analysis of tissues still more difficult. Nevertheless, although past investigations were based upon vague, incomplete and not infrequently erroneous conceptions of sexual development and the relations of plants to their environment, a great deal of experimental data was collected which outlined in general terms several trends of physiological research. Of these, perhaps the most popular proved to be those based upon studies of general chemistry, colloids, enzymes and hormones.

Physico-chemical Research on Development

All attempts made so far to discover a quantitative or qualitative relation between the physico-chemical composition and properties of protoplasm and the

advance of plant tissues in sexual maturity have given no definite results. In fact, it could not be otherwise. In these investigations, the physico-chemical studies were concerned not with the meristem, where the readjustments connected with development are localized, but with the entire plant body, various parts of which may be at different stages of physiological and morphological differentiation. Consequently, their relation to the same environmental factors and their changes is different. Moreover, it was and still is in these investigations impossible to discriminate between reserve substances and somatic substances.

Past experience may, of course, be useful in physiological studies of phasic development, but it is very difficult to co-ordinate such studies with this new trend in plant physiology. It is, on the other hand, unwise to discard them altogether, as has been done (pp. 78-9 of the review) in the research of Čaĭlahjan, Moškov and many others on the hormonal nature of development, solely because this trend "rests on photoperiodic investigations," although the writer of the review is correct in refuting (pp. 68-9) " a deep organic connexion between the phenomena of vernalization and photoperiodism," of which Cholodny (1939) speaks in his review ; indeed, the former phenomenon is an outcome of the theory of phasic development which, perforce, excludes the latter.

Physiological investigations of developmental phases attempt to trace those physico-chemical readjustments in protoplasm which transform "vegetative" tissues, through a sequence of morphological readjustments, into " reproductive " tissues. Indeed, " many internal readjustments must occur in the promeristem," at any time in the life of a plant, " but not all necessarily concern the advance in development." In order to define those physico-chemical readjustments which must precede the morphological differentiation of the meristem, it is necessary to separate these readjustments from the processes pertaining to nutrition and growth with their own particular enzyme and hormone systems. This is a difficult but not impossible task in which vernalization, particularly during seed ripening and of excised embryos at as early a growth phase as possible, may be of great value. There is another possible approach, for example, that chosen by Borgström (1939), who made a successful attempt to exclude the interference of the processes pertaining to photosynthesis.

The chemical analysis of plant tissues is usually and indiscriminately concerned with the complete range of various organic and inorganic substances. Physiologically, however, these substances fall into two main groups : the building and energy-supplying substances, such as proteins, carbohydrates, fats, mineral salts, etc., and the regulative substances, such as enzymes, hormones, vitamins and other agents functioning as physico-chemical regulators of vital processes, affecting probably not so much the chemical composition as the physico-chemical properties of protoplasm.

Chemistry and Vernalization

Chemical changes in protoplasm, as related to vernalization, have been investigated on a number of occasions with a varying degree of accuracy. Volkov, Timofeeva and Krasnoseljskaja-Maximova (p. 75 of the review) investigated the sugar content, which, according to Maximov (1913), Gassner (1918), Richter (1927), and others, increases when winter plants are exposed to lower (vernalizing) temperatures. Tolmačev (1929), Savostin and Okuncov (1934), Sapožnikova (1935) and others studied the content of soluble and insoluble carbohydrates, which suggested, if anything, a change in enzymatic activity. More interesting were the investigations of Filippenko (1936) and Konovalov (1937), who established changes in the content and composition of nitrogenous substances which were suggestive or at least conterminous with vernalization. There is also a comprehensive body of experimental data on the

chemical changes in protoplasm in relation to photoperiodic response, which cannot yet be deciphered in terms of the theory of phasic development.

All these investigations do not yet furnish a definite basis for suggesting helpful trends for further research along this line. Their main and common defect (apart from those already mentioned) is that they have dealt with plants from vernalized and unvernalized seeds during vegetation, no attempt having been made in most of them to trace the chemical alterations associated with vernalization, which ensure the completion of the thermo-phase. This has been partly due to a faulty conception of vernalization. Finally, the physiological state of tissues before and after vernalization was not checked, a fact of considerable importance in view of the possibility of vernalization during seed ripening.

Apart from this we must not attempt to explain all the vital changes in tissues entirely upon a chemical basis, thus replacing " protoplasm" with its chemical composition. Of course, protoplasm is composed of definite chemical substances and a good deal in physiological research depends upon precise knowledge of such chemical components. We must, nevertheless, not identify the conception of protoplasm exclusively with that of the chemical state of its components. Numerous examples of isomerism (ammonium cyanate and urea ; maleic and fumaric acids) and allotropy (red and white phosphorus ; diamond, graphite and charcoal) have emphasized the prime importance of structure.

Protoplasm is a distinct mechanism and as such depends greatly upon its structure. Therefore, attempts to interpret certain vital processes with complete disregard of its structure are doomed to failure. In other words, the readjustment of protoplasm is as much chemical and physical, and correlated investigations of structural changes and metabolism are essential for a successful physiological study of development. In this sense Lysenko is correct in drawing attention to the great complexity of the physiological causes of vernalization and developmental phases, and the futility of advancing chemical interpretations based upon the behaviour of one or two of the components of protoplasm.

The structural properties of protoplasm are, of course, most closely associated with the colloidal state, and changes in plasmic colloids in relation to vernalization have been directly or indirectly stressed by numerous investigators. Bassarskaja (1934, 1936), who found differences in the reaction of vernalized and unvernalized seeds to various dyes (pp. 75-7 of the review), established that "the promeristem after vernalization of the first phase plasmolysed at a higher salt concentration." In this connexion, Filippenko (1936) pointed out an increase in plasmic permeability and a difference in the temperature of coagulation. It is not surprising, therefore, that Richter and his associates (1933, 1934) established a shift in the iso-electric point of albumen-lipoids, and Vertuhova (1938) a change in the ratio between hydrophilous and hydrophobous colloids.

All these investigations are in reasonable agreement, but are at present little, if at all, connected with the somewhat conflicting results of chemical investigations, and do not provide a glimpse of those physico-chemical changes which are directly associated with the progress and completion of the thermo-phase.

From this incomplete and imperfect review of the position, one can see that physico-chemical investigations are lagging behind ecological investigations, and are in fact only of an exploratory nature, attempting to find a possible trend for further research. These investigations have been chiefly concerned with vernalization, frequently in a somewhat perverted form. Subsequent developmental phases have not yet been touched upon. This is quite natural, as ecological studies of phases must precede their physiological investigation. We have shown in previous parts of this review that the subsequent ecological phases (light-sensitive period) were incompletely,

if not incorrectly deciphered, and we may expect some unheavals in this field ; this, of course, affects the progress and success of physico-chemical studies.

Moreover, as is known, there is no direct connexion between the accumulation of chemical changes and volume of protoplasm on the one hand, with morphogenesis on the other, and there is at present a concensus of opinion as to the importance of certain regulatory substances in protoplasm. Of these chemical regulators, enzymes and more particularly hormones have been the centre of attention.

Lysenko himself has not investigated the physiological "cause" of reproduction and yet for some reason he refutes "the hormonal theory" ; nevertheless, experimental demonstrations of the participation of phytohormones in reproduction (e.g. induced parthenogenesis in experiments of Gustafson, 1936, and Sereĭskiĭ, 1938) seem to suggest that, of all hypotheses advanced so far, those based upon phytohormones are perhaps most plausible, the more so in view of the possible hormonal basis of enzymatic activities in plant tissues.

"Spring and Winter Hormone" Hypothesis

The interpretation of vernalization in terms of hormones is generally traced to Maximov who, referring to his investigations in collaboration with Pojarkova (1924-1925), and Krotkina (1929-1930), suggested that " the fundamental difference between winter and spring forms appears in the presence or absence in them of a special factor hindering the transition to the reproductive state."

This innate factor inherent, as it were, to winter forms was investigated later by Krasnoseljskaja-Maximova (1931) in relation to what was then inaccurately known as vernalization. The idea then prevailing of vernalization being a method of " converting " winter forms into spring forms has been fully reflected both in the arrangement of experiments and in the conclusions reached that from a physiological point of view vernalization actually consists in the destruction of a certain hindrance ("winter hormone") and thus "induces in a winter" form "a physiological condition leading to early flowering, which is already inherent in spring" forms (Purvis, 1939).

In these experiments the heading of spring forms was indeed delayed when part of the endosperm was replaced by pulp from unvernalized seeds of winter wheat ; on the other hand, however, a retardative effect was also recorded when the pulp was made from vernalized seeds of winter wheat. Therefore, whatever might have been the cause of the retardative effect of "winter" pulp, it was not eliminated in vernalization, as assumed by Maximov and later by Krasnoseljskaja-Maximova.

In repeating these experiments, Sereĭskiĭ and Sludskaja (1934) did not substantiate this hormonal interpretation of vernalization and still less the existence of a winter hormone, " the pulp from vernalized and unvernalized seeds having no effect on the time of earing of wheat plantules." Moreover, in the experiments "in which the halves of vernalized and unvernalized grains were exchanged in various ways, the time of heading also remained unchanged."

As has already been pointed out (cf. *Herb. Rev.* 5. 83-6. 1937 ; Whyte, 1939 ; Cholodny, 1939), some later experiments on vernalization of excised embryos (Gregory and Purvis, 1936 ; Konovalov, 1937 ; Buslova, 1938) can hardly be regarded as decisive evidence against this hypothesis, but this interpretation was based on a very faulty conception of vernalization, and can thus be disregarded in further consideration of the problem.

The Auxin Hypothesis of Vernalization

The discovery of blastanin, an auxin of endosperm (Cholodny, 1935 ; Laibach, 1935) and the investigations of Drabkin (1936) and later of others in which it was

found that this hormone was transmitted rapidly to the embryo tissues during vernalisation, gave rise to another hormonal interpretation (Cholodny, 1936, 1937, 1939), which has already been mentioned in *Herb. Rev.* 5. 83-6. 1937.

According to this hypothesis, an accumulation of this hormone (due to retarded growth in seeds at low temperatures and reduced moisture) during vernalization in embryo tissues would accelerate the subsequent development of the plants. In terms of such an interpretation, vernalization would appear as a kind of preparatory process paving the way for future development rather than as a completion of a developmental stage or stages, as is actually the case.

This auxin hypothesis was first subjected to experiment by Cholodny himself (1936); in these experiments there was indeed an example (never repeated) when an earlier heading was recorded on oat plants derived from seeds soaked for twenty-four hours in a solution containing phytohormones (hormonization).

An increase in the content of blastanin in seeds during vernalization was also reported by Sereĭskiĭ and Sludskaja (1937), but was not confirmed by Čaĭlahjan and Ždanova (1938b); in the latter experiments, on the contrary, the auxin content became reduced as vernalization progressed.

Sereĭskiĭ and Sludskaja, as well as Čaĭlahjan and Ždanova, were inclined to consider changes in the phytohormone content as being of indirect consequence to certain other processes occurring parallel to vernalization. A common aspect of these experiments was the quantitative relation between phytohormone content and growth rate.

Moreover, Tovarnickiĭ, in collaboration with Rivkind (1937) and Statkovskaja (1938), and then Čaĭlahjan and Ždanova (1938c) also experimented on hormonization on the lines suggested by Cholodny (1936, 1937), but concluded that hormonization of seeds did not affect time of heading or flowering; it did however affect the growth rate and consequently the seed and total yield of the plants, particularly when followed by vernalization (Tovarnickiĭ and Statkovskaja, 1937).

Bios and Vernalization

It is appropriate in this connexion to mention briefly the hormones of group B or bios (Wildiers, 1901) which are now known to be always present in higher plants and particularly in vigorously growing embryonic tissues. There are also grounds for believing (Suhorukov, Kling and Kljačko, 1935, Dagys, 1934-1937; Gavrilov, 1939) that their bio-catalysis in reproduction (for instance, cell division in floral organs as found by Gavrilov, 1939) has an influence far beyond the class of lower plants. Filippenko (1937) and later Wildflush (1939) found that vernalization was associated with an intensified elaboration of bios; this in Filippenko's opinion should "induce an acceleration in the completion of consecutive phases of development." This finding can account for at least some structural changes in proteins (increased content of NH_2 groups, increased mobility of proteins, etc.), as found previously by Filippenko (1936) in connexion with vernalization.

Endocrinology and Development

It may therefore be stated that neither the hormonal hypothesis of vernalization nor hormonization were confirmed in experiments; but again, and this is rather suggestive, this unconfirmed hypothesis is based upon a faulty conception which, as stated in the review (p. 74), "conflicts . . . . . with all that is known of vernalization of many plants at high and low temperatures". Nevertheless, it does not necessarily follow that we must refute any attempt at a hormonal interpretation of vernalization and sexual reproduction in general. It must be noted that in the

verification of this hormonal hypothesis the effect of vernalization and its mechanism were confused. In all these investigations, attempts were made to replace the effect of indispensable specific external factors determining the possibility of certain physico-chemical reactions and readjustments in the promeristematic cells by an increased influx of phytohormones, the action of which, as pointed out by Ljubimenko (see below and p. 79 of the review) consists in " bio-catalysis "; this last is the internal mechanism and not the cause. Thus it may be expected that an increased content of phytohormones would accelerate, but not originate those reactions and readjustments which constitute a developmental phase, if and when the environmental conditions are favourable. The experiments of Tovarnickiĭ and Statkovskaja (1938), in which the effect of hormonization was much increased when followed by vernalization, seem to support this view ; it is true that these authors did report " no conspicuous difference " in time of flowering, but the time of flowering is not indisputable evidence. Instead, they should attempt to reduce the duration of vernalization, as suggested in the review (pp. 63-4), to ascertain whether the thermophase was, or was not, under the same environment, completed more rapidly in hormonized seeds.

The many-sided physiological action of phytohormones revealed during the past decade, their undoubted participation as physico-chemical agents in various vital functions of plants, the close analogy between hormonal phenomena in plants and animals, the significance of the glands of internal secretion in the sexual life of animals, and the most recent investigations on the photoperiodic localization (of which more is given below)—all these seem to suggest that our efforts in search of the structure and nature of the mechanism of sexual development should be directed to the field of plant " endocrinology ".

The Hormonal Theory of Development

Actually, since the research of Sachs, repeated attempts have been made to elucidate a hormonal basis for sexual development ; the earliest known to us was that of Nemec (1934), who postulated a flower-inducing hormone, anthogen (cf. Cholodny, 1939). These hypothetical hormones, as Ljubimenko and Ščeglova described them (1933), " cannot affect either the form, which is determined by the structure of the protoplasm of the plant, or the succession at which one phase is replaced by another ". Therefore, if we are to accept the fact that the rapidity of development depends upon the elaboration and accumulation in the protoplasm of substances with a definite chemical and structural composition, the role of these hormones (Jost's " Reizstoffe ") consists in regulating and perhaps releasing definite reactions, that is, in what was described by Jost and many others as " Auslösung " (liberation), the decisive role remaining with the protoplasm.

A similar hormone " bio-catalysis " was postulated by Ljubimenko (1933) in relation to the photoperiodical induction by short day or darkness of " short-day " plants, the effect of which is thought to be inhibited by light. The author of this hypothesis, however, fully appreciated all the insurmountable difficulties in the reconciliation of this hypothesis with the photoperiodical response of " long-day " plants, unless another distinct hormone inherent to " long-day " plants is to be postulated. " Such a postulation will, however, draw a hard and fast demarcation between long-day and short-day plants ; meanwhile, all the available experimental evidence suggests rather that there is a quantitative, but not a qualitative difference between long-day and short-day plants " (Ljubimenko and Ščeglova, 1933). Later, in an investigation of the photoperiodical localization in *Perilla*, Ljubimenko and Buslova (1937) again postulated a hormone, presumably of Group A, manufactured in the leaves and transmitted to the terminal buds.

The localization of the incipient photoperiodical response in leaves and the transmission of the " photoperiodical stimulus " to terminal buds, particularly from " donors " to " receptors " in grafting experiments (Litvinov, 1934 ; Čaĭlahjan and others, 1936-1938 ; Moškov, 1936-1939 ; Melchers, 1936-1939 ; Psarev, 1936 ; Kuijper and Wiersum, 1936 ; Ljubimenko and Buslova, 1937 ; Hamner and Bonner, 1938 ; and others), have provided fresh circumstantial evidence in support of Sachs' idea of a " flower-forming " hormone, by virtue of which the transmission of the " photoperiodical stimulus " from the leaves, where it is conceived, to the terminal bud, where it operates, is thought to have a physical nature common to all plants and resembling phytohormones in physiological potency. Čaĭlahjan, one of the most ardent advocates of this hypothesis, introduced this hypothetical flower-inducing hormone as " florigen " which, he claims (1937), is physiologically distinct from other hormones of Group A (cf. Cholodny, 1939).

We shall refrain from examining all the evidence for and against this hypothesis, as it has been surveyed fully by Cholodny (*Herb. Rev.* 7. 223-47. 1939). To be consistent with our previous discussion, however, we shall point out that the far-reaching defect of this hormonal hypothesis of sexual development appears first of all in that the hypothesis accounts not for the entire developmental period from " fertilization to fertilization ", as one may justly expect, but only for what is known as " the transition from the vegetative to the reproductive growth ", effected as is thought by appropriate photoperiods or, in terms of the theory of phasic development, the light sensitive period. Moreover, it does so without any relation to the preceding and subsequent development. Actually, it is a hormonal interpretation of photoperiodism and shows all the latter's faults and merits. The hypothesis as advocated by Čaĭlahjan and Moškov cannot be applied even to the internal mechanism of photoperiodical induction, or to the vernalization of germinating seeds by short day or darkness.

As Cholodny rightly argues, all the investigations supporting this hypothesis have not yet provided exhaustive evidence to confirm the existence of a flower-inducing hormone ; the investigations do indeed provide some ground for the postulation of the hormonal mechanism of photoperiodic response. We fully share the view expressed by Cholodny that so far there is no need to invent a new hormone, although the existence of such is not altogether excluded.

Phytohormones and Development

It would indeed be more expedient to attack this problem while bearing in mind the multifarious actions of known hormones, for example, auxins, on the physico-chemical properties of protoplasm, which have been shown repeatedly to change as the tissues become more advanced in development ; these changes are known to " trespass the limits beyond which a quantity is converted into a quality " (Cholodny, 1937). The significance of an adequate supply of phytohormones was recently emphasized by Borgström (1939) in his experiments with a long-day variety of *Pisum* (American Wonder). Etiolated plantules formed floral primordia in a larger number and at an earlier date when adequately supplied with phytohormones (1.0 ppm.), as in Series 5, than with excess hormones (10 ppm.—Series 4), or inadequate hormones, as in Series 1 (no additional supply) and Series 6 (0.1 ppm.), emphasizing again the significance of the concentration of phytohormones.

The determination of auxin concentration in various parts of a plant under different light conditions, as quoted by Čaĭlahjan and Ždanova (1938a), cannot be regarded as convincing evidence, because the physiological condition of the tissues was not considered, while the physiological differentiation of tissues along the stem has been shown repeatedly (Lysenko, 1932, and among more recent investigations,

Eremeev, 1939). Yet the physiological action of phytohormones has been shown to depend upon the physico-chemical properties of protoplasm, for example, the effect of auxins on the protoplasm of roots and of stems, or upon hydrogen-ion concentrations of the media from which they have been extracted, as in the experiments of Rakitin and Jarkovaja (1939).

It must also be remembered that the same physiological effect can be induced by different substances as shown, for example, in experiments reported by Rakitin and Jarkovaja (1939) using various acids and phytohormones. Moreover, in these experiments the same curvature of decapitated coleoptiles was induced by solutions containing high concentrations of acid and low concentrations of phytohormones, and vice versa. Finally, it must be remembered that auxins in plant tissues are present in at least two forms, namely, the free-moving auxin and the bound auxin, the physiological state of the tissues also being of decisive importance in this connexion. There is no evidence that Čaĭlahjan and Ždanova (1938a) used any method other than that involving diffusion.

It is possible, however, to approach the same problem from a different angle, namely, by assuming some chemical and structural readjustments of the phytohormones and perhaps a physiological relation between and succession of structurally and chemically distinct hormones, for example, bios, heteroauxin, auxin *a*, auxin *b*, etc. Melchers (1939), who postulated a form of hormone (vernalin) which must precede the elaboration of florigen, seems to share this view. The field of plant endocrinology is possibly now beginning its most rapid development, and one may hope that further research in the chemistry and structure of phytohormones will help to clear up this problem.

In the hormonal hypothesis under consideration, however, there is a serious incongruity. Grafting experiments with plants having a distinct relation to photoperiods did suggest that, whatever the nature and action of the flower-inducing substances elaborated in the leaves may be, these substances are common to all plants and forms of plants. Yet, according to the hypothesis, they are manufactured by leaves of " short-day " plants in photoperiods shorter than the critical photoperiod (Čaĭlahjan and Moškov), or in darkness (Hamner and Bonner), while the same substances are formed in the leaves of " long-day " plants only in photoperiods in excess of the critical. The alternatives suggested by Cholodny (1939) are hardly plausible, yet, as Ljubimenko (1923) pointed out, it is hardly possible to postulate the co-existence of " short-day " and " long-day " hormones, thus removing the loophole for postulating two distinct substances showing the same physiological effect.

In suggesting a common developmental scheme (succession of ecologo-physiological phases), Whyte and Oljhovikov (1939 a and b) may be said to have removed this incongruity. It can indeed be assumed (Whyte and Oljhovikov, 1939b) that this hypothetical hormone is manufactured, regardless of the photoperiodic group of the plant, while the leaves are exposed to light, but only after the completion of the dark (scoto-) phase. According to this interpretation, the manufcature of " florigen " requires not only the same environmental conditions, but also the same physiological condition in the tissues ; at least, flower-forming substances, no matter when they are formed, may operate only in tissues in which the readjustments characteristic of the dark phase have been accomplished. The results of Borgström (1939) seem to support this view. It may also be remembered that, as reported by Čaĭlahjan and Ždanova (1938a), regardless of the photoperiodic group, auxin content was higher in plants grown in long photoperiods, although some failed to flower in these photoperiods.

Many examples quoted earlier in this discussion in which plants failed to respond to photoperiods also support this view. The failure to induce flowering in other careful experiments with grafting (for example, Tincker, 1938) can also be explained in these terms. Finally, the same conclusion may be deduced from Melcher's grafting experiments (1938, 1939) with biennial stock, which was induced to flower through a " short-day " annual scion in long photoperiods, in which the scion itself failed to flower.

This hormonal hypothesis must, therefore, be reconsidered, first from the point of view which presumes either structural and chemical readjustments of phytohormones, or the different action of the same hormone in tissues which are ecologo-physiologically different. It must be remembered that in no case can phytohormones replace either the environmental factors or the chemical readjustments of the tissues induced by those factors.

Yet another flaw in this hormonal hypothesis was pointed out in the review (p. 79), namely, the fact that it is possible to vernalize two consecutive phases (thermo-phase and scoto-phase) in germinating or even ripening seeds (Whyte and Oljhovikov, 1939a) seems to suggest that the leaves, which are supposed to provide the terminal buds with " florigen ", are not an indisputable instrument in the photoperiodic response of terminal buds. It is obvious that the entire body of the embryo has the ability to respond to light and darkness, as shown by McKinney and Sando (1935) in respect of the sensitiveness of embryo tissues to temperature. In other words, if florigen is indispensable in the initiation of floral organs, it must be present in seeds under this double vernalization. The endosperm is known (Laibach and Meyer, 1935 ; Cholodny, 1935), to store large amounts of auxins, but not of " florigen " ; again, Dagys (1934-1937) and later Filippenko (1937) and Wildflush (1939) found bios present in germinating seeds. The significance of auxins in floral initiation has been recently emphasized by Borgström (1939), but the possible participation of other phytohormones was not excluded in Borgström's experiments, nor was it in fact denied by this investigatior.

Enzymes and Vernalization

The hormonal system alone does not yet fully reveal the mechanism of the co-ordination of diverse physiological processes in cells. Tschirch suggested that hormones act through the enzymatic system, an idea which was further elaborated by Cholodny (1936), who postulated an hypothesis of some type of " smouldering processes ". According to this, changes in hormone content affect enzymatic processes ; some previously retarded (smouldering) may be released, others, on the contrary, may be restricted ; thus new potentials of the cells may be released.

This hypothesis, which links two trends in plant physiology hitherto regarded as independent, had, however, no effect on the studies of enzymes in relation to vernalization begun by Demkovskiĭ (1932), who investigated the behaviour of proteolase, amylase and catalase during vernalization ; the absence of any control detracted considerably from the value of this investigation, although the objective was quite correct, namely, the detection of suggestive changes in the course of vernalization. The enzymatic system was further investigated with little advance by Richter and his associates (catalases and peroxidases), Savostin and Okuncov (amylases and catalases) and Sapožnikova (" halactanase ", protease, catalase and peroxidase)—all briefly mentioned on p. 75 of the review. " Of the enzymes studied, there appears to be a suggestive difference between vernalized and non-vernalized seeds only in the activity of catalases and peroxidases ", which (in all cases except that reported by Savostin and Okuncov) increased as vernalization progressed, " but how far these

enzymes directly concern the progress of the first phase has not been decided ", or rather cannot be decided, as in the majority of investigations, " enzyme analyses were not always parallel with the test of the efficacy of vernalization ".

In some of these analyses, in fact, plants from vernalized and unvernalized seeds were used, which could provide only misleading results. Thus Savostin and Okuncov (1934) reached somewhat different conclusions, considering a reduction in enzymatic activity in germinating seeds during vernalization (observed in their experiments) to be responsible for a curtailment of the vegetative period, due to the greater rapidity of subsequent phases. They also considered that increased enzymatic activity in the seed germinating at high temperature (control) induced the same curtailment of the vegetative period, but due in this case to the greater rapidity of the early phases. It must be noted that in these experiments plants from vernalized and unvernalized seeds eared at the same time and four days earlier than plants from seed sown dry. No further comment need be made upon this hypothesis.

Both these investigations and the study of enzymes in relation to photoperiodic response suggest rather that " the trends in relative enzymatic activities can probably be correlated more closely with the type of growth which the plants are making, than with their stage of reproductive development " (Hibbard, 1937). Whatever may be the proper outlook, the relation between hormones and enzymes, as suggested by Cholodny (1936), must not be overlooked in further research.—M.A.O.

List of references will be given at end of final section.

SCANDINAVIAN LITERATURE

SWEDISH SEED ASSOCIATION, 1938

[Reviewer : R. PETER JONES]

The work of the Association has been extended materially during 1938 by taking up on a large scale plant breeding work with flax and the soybean and other plant species.

BREEDING AT SVALÖF AND ULTUNA : MEADOW PLANTS

Owing to the cold and late spring and early summer the development of meadow plants and particularly of the clover species was much retarded at Svalöf. A period of drought during the height of the summer in addition interrupted the growth of white clover for a long period. In spite of this, yield results were good and showed many varietal differences of considerable interest for breeding. The second year leys of red clover were severely attacked by the clover eelworm and clover stem rot, so that the superiority of Mercury clover in resistance to these diseases was particularly evident. An attack of clover stem rot in the white clover experiments afforded a welcome opportunity of grading the different varieties of this clover species, also with reference to resistance to *Sclerotinia*.

In the 1935 grazing experiment with strains of white clover, red fescue and smooth-stalked meadow grass a green cut was taken in 1938, and was weighed and analysed. The results gave additional confirmation to the conclusions which were drawn from ocular inspections and valuations.

The work of the hay plant department has proceeded according to the same plan as formerly. A new very comprehensive inbreeding material of timothy has been planted out during the summer. Multiplication plots of the new red clover strains referred to in the previous annual report have been very successful, so that seed in sufficient quantities is now available for experiments at Svalöf as well as at many of the branch stations. The seed production trial at Kastlösa in Öland had to be ploughed up in 1938 owing to the prevalence of weeds. Instead a trial was put down in Fredshög in south Scania and one at Bjälbo in Östergötland. Investigations in collaboration with the State Plant Protection Institute on the clover weevil were continued during 1938.

The work of the pasture plant department has been conducted on almost the same lines as previously. Four comparative trials put down in 1933, 1935, 1936 and 1937 were harvested in 1938. The above-mentioned grazing trial of 1935 has also been available.

The new grazing trial at Kungsängen, Ultuna, in collaboration with the Animal Breeding Experiment Institute, which was planned for 1938, had to be postponed for a year, as the ground there must be fallowed. New extensive inbreeding material of white clover and perennial ryegrass has been planted out during the year. The inbreeding trial with red fescue has been concluded and a series of valuable lines has been selected for multiplication or eventual crossing. A large assortment of meadow

Årsberättelse över Sveriges Utsädesförenings verksamhet under år 1938. [Report on the work of the Swedish Seed Association during the year 1938.] *Sverig. Utsädesfören. Tidskr.* 49. 183-240. 1939.

foxtail has been planted out for observation and selection. A comparative strain trial with different strains of *Phalaris arundinacea* has been laid down for the first time.

Trials with sweet lupin comprising partly comparison between blue and yellow, partly a number of different cultivation measures, have been carried out at several centres in south and middle Sweden. The results have further confirmed the value of the plant for the sandy soils of south Sweden and have furnished guidance as to cultivation technique in the country itself. The hybridization work which had been begun has been continued, but has been retarded hitherto by difficulty in obtaining suitable initial material for crosses. It is now hoped that by means of exchange of material with the German Plant Breeding Institute at Müncheberg, old land sorts of bitter lupin will be obtained for continued selection.

Soybean

During the year breeding work with this plant together with maize and some other foreign cultivated plants has been organized in a special department. Work with the soybean has consisted mainly in a testing of the very large number of foreign varieties. Observation trials with a larger or smaller number of these varieties have been laid out at many centres in addition to Svalöf: at Fredshög, in Öland and Gotland, at the branch stations in Kalmar, Linköping, Skara and Ultuna, and also on individual farms in Scania, Blekinge, Halland and Småland.

Breeding work during the year has consisted in selection of single plants partly from the European material—a large portion of the varieties collected is not pure but consists of still segregating breeding material—partly from populations obtained chiefly from Manchuria, and also in crosses between different varieties. The object of this breeding work in the first place is to obtain early strains, which will be able to ripen with certainty every year. For this purpose types still earlier than those now existing are required, and crossing between these with a view to obtaining transgressively early progenies is therefore one of the most important branches of Swedish breeding work.

Raising of the yield is the second important object. In the existing soybean varieties in cultivation in Sweden this is particularly low in comparison with that of other cultivated plants. Progress already made, for example, in German plant breeding work, suggests, however, that there are great possibilities of increasing the yielding capacity.

Other important objects of breeding are further improvement of quality—in particular the fat content, which in cultivation in northern latitudes tends to fall—the production of strains with a habit of growth suitable for cutting by machine—in this connexion it is important that the plants should not be too low, and that the pods should be situated at a certain height above the ground—and also the attainment of resistance to certain diseases, to judge from the experiences of the first year virus diseases and *Peronospora* in particular.

Sowing of the soybean took place during the first week of May, which possibly was unnecessarily late, in view of the fact that comparative time of sowing trials showed better development and earlier ripening in two experimental treatments which were sown on April 13 and 23. Owing to the soybean plants' ability to tolerate frost it should not generally speaking be necessary to postpone sowing on account of risk of night frosts. On the other hand soybeans require a certain minimum temperature of the soil in order to germinate, so that too early sowing, if the soil is cold, does not result in more rapid establishment.

Some of the varieties tested rotted in the soil with early sowing, but the majority—among them the earliest—were able to tolerate it, and showed correspondingly earlier ripening and higher yield. Owing to the heterogenous character of the seed

sown, establishment was in part poor, and the stand, as far as a large number of varieties were concerned, thin.

Owing to the cold and wet weather during the early part of the summer, growth, which even normally in the earliest stages is very slow, was further delayed, and flowering even of the earliest varieties did not begin until the middle of July. Ripening of these early varieties took place about September 20. Owing to the mild autumn, which allowed the material to remain out up to the beginning of November, a ripe crop of most of the varieties in the assortment was obtained.

During the first half of June, which was wet, a severe attack of *Peronospora* occurred. Considerable varietal differences in resistance were apparent. A large portion of the assortment at Svalöf was in addition seriously attacked by virus diseases, although here too marked varietal differences appeared, certain varieties showing themselves to be quite unaffected by the diseases.

The yield from the different trials naturally varied greatly and too much importance should not be attached to it owing to the lack of uniformity in the trials. The earliest and highest yielding varieties gave, however, both at Svalöf and in particular in Öland and at the Kalmar Branch Station a comparatively satisfactory yield of fully developed, fine seeds. This applies in particular to the black and the brown seeded varieties, while the yellow seeded on the other hand showed a tendency to produce qualitatively poorer seeds.

A very large number of crosses were carried out during the summer, and the results, taking into consideration the very great difficulties inherent in the work, have been satisfactory.

Preliminary investigations have also been carried out on the dependence of the different varieties on length of day in regard to time of flowering and ripening.

Department of Genetics

During 1938 work has been carried on in the main with wheat, rye, barley, timothy, cocksfoot, smooth-stalked meadow grass and potatoes. The production of rye × wheat hybrids, the cytological study of the reduction divisions in the *Triticale* forms, and the production of tetraploid types of rye and barley by the temperature treatment method are the concern of the Imperial Bureau of Plant Breeding and Genetics, and will not be discussed here.

Work with the different grass species has in the first place related to timothy and special investigation of progenies from high-chromosomed timothy plants obtained by the so-called twin seedling method. The progenies have been studied particularly with reference to yield and fertility and the connexion of these with the plants' chromosome number. Further a series of new crossings has been carried out between selected high-chromosomed mother plants and also new sixty-three-chromosomed twins have been bred from particularly valuable initial material (the Meadow Plant Department's best clones.) Finally a large part of the harvested material has been handed to the Chemical Department for nutritive value analysis.

In addition to high-chromosomed timothy obtained by the twin method, the Department has also continued work with products of crosses between ordinary timothy and pasture timothy. This work like the investigations with cocksfoot and smooth-stalked meadow grass has been continued in the main along the same lines as previously.

Finally mention must be made of the so-called colchicine method for production of high-chromosomed plant forms preliminarily tested particularly with cereals and some species of grasses. Results have hitherto in the main been negative, but the positive results which have been obtained at the Institute of Genetics (with other material) make continued experimentation of this kind desirable.

NORWEGIAN LATE-FLOWERING RED CLOVER

[Reviewer: R. PETER JONES]

In the older rotation systems in Norway, according to S. Hasund,* red clover was grown as an annual, a practice which has in part persisted to the present time. This was mainly due to the fact that the clover grown then was generally only slightly winterhardy. It was early flowering and "in the main" an annual.

When seed production was begun in Norway, it was found that some variants over-wintered fairly well, and these varieties were late-flowering. Examples which can be mentioned are Toten clover and Molstad clover. When Norwegian plant breeders some years ago began to study the different types which appeared in the clover meadows—in particular the work of H. Wexelsen in this connexion should be noted—the question arose, where and how Norwegian late-flowering and comparatively winterhardy red clover varieties originated. Had they come into being in recent times during their cultivation in Norway, or had they come from abroad with imported seed—and if so, where from?

About the year 1800 the market gardeners in the towns in Norway sold seed of meadow plants. This seed was often imported from Holland, but was also sometimes obtained from Denmark and Germany. The question is then whether late-flowering and comparatively winter-hardy variants occurred in the foreign red clover seed which was distributed throughout Norway about the year 1800 and later.

It is most probable that these variants were to be found even then in the imported red clover seed. In the Danish journal "Nye Oeconomiske Annaler" for 1815 the editor, Professor Chr. Olufsen, wrote an article, "On pastures and their improvement," in which he emphasized that cultivated red clover, which originally is from Brabant and is therefore called Brabant clover, has *two varieties, the early and the late.*

As a reader of the journal requested further information about the "two varieties" of red clover, a circumstance of which he was completely ignorant, the editor gave the following information in the volume for 1816.

"When I recorded this observation, I thought the fact was far more generally known than I find it to be; I am now led to believe that but little heed is paid to it excepting in Lolland, where my attention was first directed thereto. I have now investigated it in several places there and in Falster, and I have been convinced that there are actually in cultivation two varieties of red clover, differing slightly from one another from the economic point of view; they cannot easily be distinguished by botanical characters, but their habit shows distinct deviation.

The one of these varieties, the early—also called summer clover—grows high, without many side branches, which remain close to the main stem. It can be cut for green fodder long before the other variety and is therefore useful for stall feeding; it gives two hay cuts, and both green and as hay it is a finer fodder than the other variety. It is readily injured during the winter and is often killed by frost. It appears as if this variety is characterized by lighter colour of the leaves and stems.

The late variety is called in Lolland and Falster winter clover. It comes into growth later than the other, is less erect, has many side branches, can rarely be cut for hay more than once, but gives a large yield and on the whole more than the early variety; it is alleged that the stems are stiffer and that the leaves are still more inclined to fall off. It is not easily killed by frost, and persists longer than the other variety.

---

*HASUND, S. Vår seintblomstrende raukløverslag. [Our late flowering type of red clover.] *Tidsskr. norske Landbr.* 46. 285-7. 1939.

How these two varieties have arisen is a question, the answer to which lies in the same darkness as conceals the origin of all varieties. Nowadays a farmer does not always know where his clover seed actually comes from ; in consequence he does not know the climate, the soil, the method of cultivation which has contributed to change the original plant. However, it is not unlikely that the practice of using second year's clover or the second cut of first year's clover for seed may have had a considerable effect in weakening the clover, and that early clover is a plant weakened thereby, which is confirmed by its lighter colour, its fewer side branches, its poor winter resistance and its shorter persistency (?).

It appears as if it is the summer clover which is nowadays the most commonly grown. For the closer investigation of observant farmers, I put this question : Should not the recognized fact that red clover nowadays fails more frequently than previously, and that it generally is less persistent be attributed to the circumstance that we now grow mostly summer clover, instead of growing mostly winter clover as formerly."

The author's theory that early clover originated by a weakening of the originally more hardy and late-flowering clover can be disregarded. It is provisionally sufficient to state that the red clover which was grown in Denmark at the time was a mixture of two or more lines or variants, of which one or more was early and non-persistent, one or more late-flowering and more winterhardy. That the red clover seed which was imported into Norway was a similar mixture can be taken for granted. But in Norway it was not general to grow clover as an annual, it was left down both for two and more years or as long as it could maintain its position. If then preferably seed was taken from the second year's clover—thus from that which had managed to overwinter—the early variant or variants in the mixture gradually disappeared and there was formed a local variety of red clover which was late flowering and comparatively winter-hardy. This seems to be the most likely explanation. In any case there appears to be no reason to doubt that the best Norwegian varieties of red clover were imported from abroad as an admixture in commercial seed.

PARASITES OF RED CLOVER

[Reviewer: R. PETER JONES]

It frequently happens in Scania in South Sweden that leys are a failure as far as legumes are concerned. Among the most important causes of this, according to E. Åkerberg, are attacks by plant and animal parasites [Växt- och djurparasiter i försöken med rödklöver vid Weibullsholm under åren 1932-38 (Plant and animal parasites in experiments with red clover at Weibullsholm during the years 1932-38.) *Landtm. Svenskt Land.* 23. 816-7. 1939]. In how high a degree these, in comparison with other factors, constitute the reason for legume-deficient Scanian leys it is of course difficult to say. Some insight into the effect of different factors is, however, given by experimental work, when this follows and investigates the causes of changes in density of stand etc.

It has been possible to ascribe in a high degree the differences in stand and yield in the experiments on which Table 1 is based to attacks by various parasites. As soon as such attacks ceased, stand and yield were satisfactory in both first and second year leys. On the average of the experiments with the best stand (i.e., least attack) red clover in the main cut of the first year ley gave more than 29,000 kg. green mass per hectare. Corresponding second year leys gave on the average no less than 80 per cent of it. In the experiments in which severe parasitic injuries occurred, the yield was different. The first year ley in these gave on the average 12 per cent less than the best, and the second year ley gave only 1/3 of the *best* first year ley and slightly more than 40 per cent of the *best* second year ley. In one first year ley and two second year leys of the experiments showing the most pronounced thinning out the parasites had practically completely blighted and killed all the red clover plants. These injuries by parasites in the red clover experiments at Weibullsholm were mainly due to attacks of clover stem rot and of the clover eelworm.

The results from Weibullsholm cannot of course in regard to the main causes of the disappearance of red clover in the first and second year leys which were found there be considered to be representative for Scania, particularly as the investigations apply only to late red clover. But they are in agreement with general experience within the province, that it is above all through the injury caused by certain parasites that first year and in particular second year leys deficient in legumes are so frequently met with. This has also been emphasized repeatedly previously by Nilsson-Ehle, Sylvén, Nilsson-Leissner and many other investigators.

Breeding has largely been directed to the production of strains resistant to the parasites mentioned. That this can be done is shown by Mercury red clover bred by Sylvén.

In the sown red clover stand at Weibullsholm rot and eel-worm caused frequent and severe ravages. They also attacked the planted out breeding material (distances between plants 50 × 50 (or 75) cm. and 15 × 20 cm.). But this material showed also attack of a particularly serious nature by a third red clover parasite, *Gloeosporium caulivorum*. The attack begins in the early summer but becomes most severe during the height of the summer on the aftermath or on plants left for seed.

In the 1936 planted out material about 30 per cent of the plants had been killed in the second year ley. Still more severe was the attack in the 1937 material. Here as early as the first cut of the first year ley 30 per cent of the number of plants had disappeared and at the second cut nearly half. Similar injuries are mentioned by J. Eriksson, who reports cases where 25 to 50 per cent of the yield was destroyed.

It might be of general interest to know what differences in resistance to *G. caulivorum* various strains of red clover showed (Table 2).

In the 1936 planted out material Spannarp was taken as standard. The two other strains R 398 and R 51 derive from collected material of unknown origin. In the first year ley the stands are in the spring practically equal for the three strains, while Spannarp in the autumn of this year and particularly in spring and autumn in the second year ley shows an appreciably thinner stand than R 398 and R 51. In the autumn in the second year ley Spannarp has only about 50 per cent of the number of plants of the two other strains.

As already mentioned it has been possible to ascribe the thinning out in this plant stand to a large extent to attack by *G. caulivorum*, and the figures cited indicate that R 398 and R 51 show no mean resistance to this parasite.

Confirmation of this power of resistance was afforded by the 1937 planted out material. Instead of Spannarp, Mercury bred from that strain was taken as standard in this experiment. As a fourth strain, R 3109 from the well-known Danish strain Øtofte medium-early is included in the table. Even in the year of planting out *G. caulivorum* began its work of destruction and this was continued in the first year ley.

That thinning out was considerable is shown by the relative figures quoted. R 3109, which for the rest is a valuable strain, has in the autumn of 1938 scarcely 1/4 stand on the plot with the larger distance between the plants and only 2/5 stand on that with the smaller distance between the plants. Mercury also is severely thinned out, while R 398 and R 51 show strikingly good stands. The latter has approximately 4/5 of the stand remaining in the autumn in the first year ley. Interesting too is the observation that the two very severely attacked strains R 3109 and Mercury both in autumn and spring have thinner stands on the plot with the larger distance between the plants than on that with the smaller distance, while the reverse is the case with the resistant R 51.

The figures quoted show that also in the combating of *G. caulivorum* breeding has prospects of working successfully with a view to producing resistant strains. The two strains R 398 and R 51 have also shown themselves but slightly susceptible to rot. These two strains like the others referred to were planted out during 1936 and 1937 on a farm near Ljungbyhed. Here the material was only lightly attacked by *G. caulivorum* but the more by rot. In the 1936 material Spannarp after the first winter had only 64 per cent plants remaining, R 398 and R 51 on the other hand had 96 per cent. In the material set out in 1937, the four strains Mercury, R 3109, R 398 and R 51 were already known from previous experiments to be resistant to rot, and this was evident from this experiment also. The strains showed no certain differences in stand and this was on the average approximately 80 per cent of that set out. The other strains had only 46 per cent of the original plants left.

It would be of particular interest to investigate to what extent clover seed plots in Scania are exposed to attack by this fungus.

That there are differences among strains in resistance to *G. caulivorum* in the same way as with those referred to is definitely known from other quarters. But the material produced may serve as a good example of what breeding can accomplish in the control of this scourge also.

CONFERENCES

New Zealand Grassland Association

The Seventh Annual Conference was held at Hamilton, on October 5-7, 1938, under the presidency of A. H. Cockayne. A mimeographed report contains the papers read. Abstracts will appear in *Herb. Abstr.* 9. No. 4. 1939.

E. B. Glanville. Establishment and management of pastures on gum land carrying scrub.

C. S. Dalgliesh. Establishment and management of pastures on pumice land carrying scrub.

H. E. Annett. Waikato pastures.

J. E. Bell. Pastures for wet land.

R. P. Connell. Some features of current land utilization.

P. W. Smallfield. Review of topdressing in the Auckland Province.

S. Smith. Rehabilitation of deteriorated land in the Waikato.

A. B. Jordan. Rehabilitation of deteriorated land in the King Country.

P. S. Syme. Technique of topdressing experiments.

N. H. Taylor. Some aspects of erosion of farm lands.

Wm. Riddett. The relation of pastures species to quantity and quality of milk.

J. W. Woodcock. Harrowing of pastures.

The 1939 Conference was held at Christchurch from Oct. 31 to Nov. 2 inclusive. While preference was given to papers dealing with agronomy in the South Island, a number of papers of national scope or application were also included. Further details will be given as soon as they are received.

Institute of Botany, Ukrainian Academy of Sciences.

A scientific session was held from March 21 to 26, 1939, at the Institute of Botany, Kiev, and was attended by some 107 persons, thirty-three of whom came from other botanical institutions in Kiev, Kharkov, Moscow, Vinitza, and Chernigov (*Visti. Akad. Nauk.* URSR. 1939). Relevant papers included the following.

A. A. Sapegin (member of AN USSR = Acad. Sci. Ukr. S.S. Republic, Kiev) reported on the determinative period already established in the development of generative organs in wheat. Early in the photo-phase, as a result of certain preparatory readjustments in the promeristematic tissues, the floral ridges (primordia) are laid down and the cells of the future spike begin rapid growth and elongation. External factors (X-rays, temperature, moisture, nutrition, etc.) during this determinative period may cause a decrease or an increase in the number of spikelets on an ear, and thus in the ultimate seed yield. N. N. Griško (member of AN USSR) read a paper on the problem of the state and maintenance of sexually altered forms of hemp, discussing in this connexion simultaneously ripening forms, and the characters of sexually altered forms with reference to the classification of hemps (cf. *Herb. Rev.* 6. 180. 1938). A. S. Okanenko (Institute of Sugar Industry, Kiev) reported on the grafting of various beets, emphasizing the importance of enzymes in the manufacture of inorganic matter in the grafts, which comprised leaf rosettes of sugar beets grafted on to the root stock of fodder beets and vice versa. In his report on the effect of the spectral composition of light on phasic development of plants (tomato, strawberry, *Nicotiana*, etc.), A. A. Kuzjmenko pointed out that the completion of the photo-phase is determined chiefly by the intensity of light. In most of the plants tested, the long-wave portion, as distinct from the short-wave portion, caused an acceleration in development and growth. A. Sereĭskiĭ gave a critical review of the significance of hormonal substances and fructa-

tion, beginning with the research of Hofmeister and Darwin, and concluding with some of the most recent physiological research. Ja. S. Modilevskiĭ (corresponding member of AN USSR) and R. A. Weiles discussed the ontogenesis of wheat in the light of cytological investigations, dealing with sexual development from the swelling of seed to the ripening of the next seed crop.

Other reports included Ju. D. Kleopov on the inter-relation between forest and steppe, E. M. Bradis on the classification of turf species, and M. I. Kotov on the migration and settlement of plants in the Ukraine.—M.A.O.

Royal Society of Canada

The Annual Meeting was held at the University of Montreal from May 22 to 24, 1939 (*Science*, 90. No. 2329. 159-61. 1939). Contributions included twenty-nine botanical papers in the Section of Biological Sciences, to which Dr. J. M. Swaine delivered the presidential address on "Scientific research as the key to progress in agriculture." Dr. N. H. Grace reported upon the relative physiological activity of the members of a series of naphthyl acids when applied to plant cuttings. Factors affecting stomatal movement in the dark were described by J. H. Whyte. That increased permeability of the host accompanies increased susceptibility to parasites and diseases in plants was shown by F. S. Thatcher. The importance of boron for normal cell division, enlargement and maturation of plants was described by J. G. Coulson and R. O. Lachance, while studies related to winter hardiness of plants were reported by J. Levitt and D. Siminovitch.

Genetical papers (W. P. Thompson, F. H. Peto, H. G. F. Sander, G. B. Wilson and H. B. Newcombe) dealt with sterility and chromosome segregation in wheat, the production of fertile amphipolyploid plants from sterile hybrids of *Triticum* species and *Agropyron glaucum* by temperature and colchicine methods, and similar matters.

American Society of Agronomy

The twenty-third annual meeting of the Western Branch was held at Davis and Berkeley, California, from June 6 to 8, 1939. Papers included the following (see *J. Amer. Soc. Agron.* 31. 663-4. 1939).

H. E. FINNELL, Oregon State College. Production of sugar beet seed.

IAN A. BRIGGS, University of Arizona. The effect of differences in soil moisture on the yield and quality of alfalfa seed.

D. D. HILL, Oregon State College. The effect of frost and scald on the germination of barley.

R. J. EVANS, Utah State Agricultural College. Recent developments in our weed research programme.

J. P. CONRAD, University of California. Determining by plant response the retention of nutrient ions by soils.

G. R. McDOLE, Pacific Northwest Region, Soil Conservation Service, U.S.D.A. The role of straw in erosion control.

F. G. PARSONS, University of California. Some distinctive features of the seed certification programme in California.

American Association for the Advancement of Science

A meeting of this Association was held in Milwaukee, Wis. from June 19 to 24, 1939 (see report in *Science*, 90. No. 2325. 45-55. 1939).

The American Society of Plant Physiologists co-operated with the Section on Botanical Sciences in a symposium on photoperiodism, under the presidency of A. E. Murneek. "W. F. Loehwing presented an introductory statement of the current status of this concept, emphasizing the need of modification in ideas concerning 'flowering' and its associated physiology. The significance of the appearance of flower primordia and differentiation of sexual parts was stressed. Differences of photoperiodic requirement for the inception of these developmental phases were noted and the inadequacy of the hormone concept to account for sexual differentiation was pointed out. Karl C. Hamner discussed the photoperiodic responses of several species in relation

to the theory of hormone function in the flowering of plants. He presented evidence that, according to species, flower development may be initiated in either light or darkness or in combination of the two. Melcher's concept of the functioning of at least two hormones in the response of *Hyoscyamus* was considered possibly applicable to the species here concerned.

" R. H. Roberts reported that anatomical studies offer evidence for structural characteristics which follow blossom induction. He suggested that these may account for continuance of effects from short-term photoperiodic treatment. Inducing of blossoming by cooling a portion of the stem was interpreted as indicating that this organ may participate with the leaves in causing flowering."

The report of the twenty-third meeting of the Pacific Division of the Association and associated Societies held at Stanford University during the week commencing June 26, is given in *Science*, 90. No. 2328. 123-31. 1939. The programme included a joint symposium between the Western Section of the American Society of Plant Physiologists and the Botanical Society on " Translocation of solutes in plants," and another on "Growth" (growth in meristems, nutritional factors involved, and role of vitamin B and auxin).

Swedish Seed Association

The annual meeting of the Association was held on July 18, 1939, on this occasion at the Ultuna Branch Station, near Uppsala, where the Branch Station's new buildings were ready for occupation. (E. Trotzig. Sveriges Utsädesförenings årsmöte. [Annual meeting of the Swedish Seed Association.] *Svensk Frötidning.* 8. 89-92. 1939.)

The Association conducts its breeding work at Svalöf and at nine branch stations distributed over the whole country. The Director, Professor A. Åkerman, emphasized the importance of the work of the branch stations.

Dr. Torssell gave an account of the work done at Ultuna and the results obtained there. Ultuna clover and Ultuna lucerne are well known and are now used as material for continued breeding.

The meeting was followed by an excursion through Västmanland. A visit was paid to Skultuna farm, which is of particular interest as Sweden's largest producer of timothy seed.

International Society of Soil Science

One of the three symposia dealing with different phases of soil microbiology which formed the subjects of the meetings, at New Brunswick, N.J., of the Third Commission of the International Society of Soil Science (August 30-31, 1939) was that on Legumes and Legume Bacteria. (*J. Amer. Soc. Agron.* 31. 367. 1939.)

The papers read were :

- A. I. Virtanen. Symbiotic N-fixation by leguminous plants.
- K. V. Thimann. The physiology of nodule formation.
- R. Nilsson, G. Bjalfve and D. Burström. Growth factors for Rhizobia.
- W. W. Umbreit and P. W. Wilson. Studies on the mechanism of symbiotic nitrogen-fixation.
- F. Allison. Respiration rates of Rhizobium ; their estimation and significance.
- A. Demolon. Bacteriophage and the growth of legumes.
- H. Katznelson. Bacteriophage and the legume bacteria.
- H. G. Thornton. Strains of nodule bacteria.
- J. K. Wilson. Symbiotic promiscuity in the Leguminosae.
- L. T. Leonard. Bacteria associated with *Gleditsia triocanthosy* [?].
- P. L. Gainey and J. T. Kroulik. The nitrogen fixing efficiency of *Rhizobium meliloti* endogenous [? indigenous] to Kansas.
- W. A. Albrecht. Some soil factors in nitrogen-fixation by legumes.
- O. N. Allen. Rhizobium-leguminous plant relationships within the cowpea group.
- A. L. Whiting. Variations in the adaptability of strains of *Rhizobium leguminosarum.*

Fifth International Grassland Congress

Although the above Congress has had to be postponed, in agreement with the Bureau of the International Grassland Congress Association iu Leipzig, the full programme of papers has been received from the Secretary for publication in *Herbage Reviews*. No decision has yet been made as to the date upon which the meeting will be held.

PROGRAMME

SECTION I. SOILS AND MANURING

President : Prof. Ir. J. Hudig, Wageningen, Netherlands.
Vice-Presidents : Prof. Dr. N. von Bittera, Magyar Ovár, Hungary.
Prof. Dr. J. A. Hanley, Newcastle-on-Tyne, England.

* * *

1. The Application of Organic Manures to Grassland.
   Ir. G. Lienesch, Schagen, Netherlands.
   Dr. E. Truninger, Liebefeld, Switzerland.

2. Importance of the Soil Structure for Grassland and Means of Improving it.
   Ir. O. J. Cleveringa, Zutphen, Netherlands.
   Dr. H. Kannenberg, Neuhammerstein, Germany.

3. Herbage of Composition Unsuitable for Grazing Animals.
   Prof. Dr. B. Sjollema, Utrecht, Netherlands.

4. The Control of Pica by Manuring with Copper Sulphate.
   Prof. Dr. W. Nicolaisen, Kiel, Germany.

5. The Use of Nitrogenous and Organic Manures on Grassland.
   Prof. Dr. L. Rinne, Tartu, Esthonia.

6. Productivity Studies on Transvaal Veld.
   Thos. D. Hall, D. Meredith and S. M. Murray, Johannesburg, South Africa.

7. Infiltration Experiments in the Wieringermeer.
   Ir. C. Kalisvaart, Medemblik, Netherlands.

8. Influence of the Weather on the Spring Growth of Grassland.
   Prof. Dr. C. Brouwer, Jena, Germany.

SECTION II. GENETICS, PLANT BREEDING AND SEED PRODUCTION.

President : Prof. Ir. C. Broekema, Wageningen, Netherlands.
Vice-Presidents : Prof. K. T. Kolbai, Keszthely, Hungary.
Prof. Dr. O. Valle, Tammisto, Finland.

* * *

1. Significance of Cytology for the Breeding of Herbage Plants.
   Prof. Dr. Arne Müntzing, Svalöf, Sweden.
   Prof. Dr. Dontcho Kostoff, Moscow, U.S.S.R.

2. The Breeding of Grasses and Clovers for Permanent Pastures in Scandinavia.
   H. Wexelsen, Hjellum, Norway.
   Collaborators : H. N. Frandsen, Øtoftegaard, Denmark.
   Dr. G. Nilsson Leissner, Svalöf, Sweden.
   Dr. O. Valle, Tammisto, Finland.

3. Indigenous Strains of Grasses and Clovers in North Sweden.
Dr. Frederick Nilsson, Svalöf, Sweden.

4. Genetics of White Clover and its Bearing on Practical Breeding.
Dr. R. J. Garber and Dr. S. S. Atwood, State College, Pennsylvania, U.S.A.

5. Technique for the Production of Seed of Clover Strains.
Gwilym Evans, Aberystwyth, Wales, Great Britain.

6. Technique for the Production of Seed of Grass Strains.
Dr. W. Fischer, Landsberg/Warthe, Germany.

SECTION III. GRASSLAND SOCIOLOGY AND ECOLOGY. BOTANICAL ANALYSIS OF GRASSLAND.

President : Prof. Dr. E. Klapp, Bonn, Germany.
Vice-Presidents : Prof. Dr. C. Regel, Kaunas, Lithuania.
Ir. Ch. Vezin, Paris, France.

* * *

1. Report of the Committee for the Study of Methods of Botanical Analysis.

2. Sociology and its Significance for the Study of Grassland.
Dr. D. M. de Vries, Wageningen, Netherlands.

3. Sociology of the Meadows of Northern Europe.
Prof. Dr. C. Regel, Kaunas, Lithuania.

4. The Importance of the Species in Grassland.
Prof. Dr. E. Klapp, Bonn, Germany.

5. The Genus *Agrostis* and its Significance for Agriculture.
Dr. F. T. Wahlen, Zürich-Oerlikon, Switzerland.

6. The Botanical Composition of French Pastures, Fifty Years Ago and Now.
Ir. Ch. Vezin, Paris, France.

7. Salt Pastures and Changes that take Place after Reclamation.
Dr. K. Zijlstra, Groningen, Netherlands.

8. Botanical Collections as a Basis of Grassland Study.
Dr. J. von Piukovich, Budapest, Hungary.

SECTION IV. MANAGEMENT AND UTILIZATION OF PASTURES. QUESTIONS OF FARM ORGANIZATION.

President : Ir. G. Veenstra, Wageningen, Netherlands.
Vice-Presidents : Dr. G. Giöbel, Ultuna, Sweden.
Prof. Dr. D. B. Johnstone Wallace, Ithaca, New York, U.S.A.

* * *

1. Temporary Leys or Permanent Pasture ?
Prof. Sir R. George Stapledon, Aberystwyth, Great Britain.
Prof. Dr. F. Falke, Arendsee, Altmark, Germany.

2. MIXTURES FOR SHORT LEYS.
Prof. Axel Pedersen, Copenhagen, Denmark.

3. FREQUENCY OF MOWING AND GRAZING IN CONNEXION WITH THE NUTRIENT RESERVES OF THE SOIL AND THEIR DEPLETION.
Dr. F. König, Steinach, Germany.

4. THE IMPORTANCE OF LEGUMES FOR THE IMPROVEMENT OF GRASSLAND IN THE HUMID REGIONS OF THE UNITED STATES OF AMERICA.
Prof. Dr. D. B. Johnstone-Wallace, Ithaca, New York, U.S.A.
Dr. A. J. Pieters, Washington, U.S.A.

5. THE COST OF MILK PRODUCTION IN THE NETHERLANDS.
Dr. H. J. Frankena, Wageningen, Netherlands.

6. GRASSLAND PRODUCTIVITY UNDER CONDITIONS IN SWITZERLAND.
Dr. A. Kauter, Zürich-Oerlikon, Switzerland.

7. TETHERING.
V. Steensberg, Copenhagen, Denmark.

8. THE NUTRITIVE VALUE OF THE HAY FROM WATERED MEADOWS.
MM. L. Maume, L. Alabouvette, Kunholtz-Lordaz and L. Monteil, Montpellier, France.

SECTION V. FODDER VALUE OF PASTURES. FODDER CONSERVATION.

President: Prof. Dr. E. Brouwer, Wageningen, Netherlands.
Vice-Presidents: Prof. Dr. H. Møllgaard, Copenhagen, Denmark.
Prof. V. Vezzani, Turin, Italy.

* * *

1. THE NUTRITIVE VALUE OF GRASSLAND CROPS, COMPARED WITH OTHER CROPS.
Prof. O. McConkey, Guelph, Canada.

2. NUTRITIVE VALUE OF HERBAGE, FRESH AND CONSERVED.
Prof. Dr. E. Brouwer, Wageningen, Netherlands.

3. THE ARTIFICIAL DRYING OF GRASS.
E. J. Roberts, Bangor, England.
Collaborators: Prof. Dr. E. Crasemann, Zürich, Switzerland.
Dr. H. J. Frankena, Wageningen, Netherlands.
T. G. Lundström, Ultuna, Sweden.
Prof. Dr. von Sybel, Jena, Germany.
H. L. Westover, Washington, U.S.A.

4. RECENT EXPERIENCE IN THE USE OF SWEDISH AND OTHER FRAMES FOR GRASS DRYING.
Prof. Dr. W. Kirsch, Königsberg, Germany.

5. NET ENERGY OF A.I.V. SILAGE.
Prof. Dr. H. Møllgaard, Copenhagen, Denmark.

6. The Use of Formic Acid for the Ensilage of Grass.
   Dr. W. Speer, Ludwigshafen, Germany.

7. Trials of Chemical Aids to the Ensilage of Grass.
   Dr. J. C. de Ruyter de Wildt, Hoorn, Netherlands.

8. The Acidity of Silage Made by Different Methods.
   V. Vezzani and E. Faraggiana, Turin, Italy.

9. The Fat Content of Grasses and Clovers.
   Prof. Dr. R. Salgues, Brignoles, France.

SECTION VI. ESTABLISHMENT AND UPKEEP OF TURF FOR SPORTS AND LANDING GROUNDS.

President : R. B. Dawson, Bingley, England.
Vice-President : John Monteith, Jr., Washington, D.C., U.S.A.

* * *

1. Problems of Turf Upkeep and Investigations in Progress.
   R. B. Dawson, Bingley, England.

2. The Genus *Agrostis* and its Significance for Turf.
   John Monteith, Jr., Washington, D.C., U.S.A.

3. The Significance of the Genus *Festuca* for Turf Production.
   N. L. Ferguson, Bingley, England.

4. Establishment and Maintenance of Airport Landing Grounds and Playing Fields.
   Prof. Dr. W. Freckmann, Berlin, Germany.

5. A Study of the Soil of Some Football Fields.
   Dr. D. J. Hissink, Groningen, Netherlands.

6. Some Factors of Turf Management.
   R. B. Ferro, Bingley, England.

7. Fungous Diseases of Turf.
   T. A. C. Schoevers, Wageningen, Netherlands.

8. Weed Control on Sports Turf.
   R. P. Libbey, Bingley, England.

Seventh International Botanical Conference

The Organizing Committee of the Seventh International Botanical Congress which was to be held in Stockholm, 1940, has, on account of the present international situation and in conjunction with the Swedish Government, decided to postpone all preparations for the Congress until further notice. This means that there will be no Congress during 1940. The Organizing Committee and its Executive have not, however, been dissolved, but will continue in office, and will, at the first opportunity, communicate with the leading botanical circles in different countries with a view to ascertaining a suitable time for the Congress to be held.

ANNOTATIONS

Sweden (485)

Swedish meadow plant breeding

At the present time one of the most important problems of plant breeding is the improvement of the quality of Swedish cereals. In potato breeding, too, important questions call for attention.

In the breeding of meadow plants (A. Åkerman. Svensk växtförädling. [Swedish plant breeding.] *Svensk Frotidning*. 8. 88-9. 1939) it is especially desirable to produce strains of red clover suitable for different areas and as resistant as possible to clover stem rot and clover eelworm attack. It should also be possible to improve the other meadow plants, and here attention should be paid to new demands which the cultivation material must satisfy with a more general transition to artificial drying of the ley crop. Extensive breeding work with the soybean has been initiated at Svalöf to produce as soon as possible high yielding varieties, at least worth cultivating in the event of the country's supply from abroad being cut off.

At certain of the branch stations of the Swedish Seed Association new buildings are needed, and the mechanical equipment should be improved and added to. At Svalöf it is highly desirable that the chemical department, the investigations of which are assuming still greater importance in connexion with breeding for quality, should be extended.

Another important desideratum is the working out of the simplest and most rational methods of selection. For this, comprehensive plant physiological investigations are necessary, and the Swedish Seed Association is now able to conduct such researches on a small scale. These have hitherto related to the winter-hardiness of plants and the factors which influence it, and the effect of length of day on the growth rhythm of plants. It is hoped that it will soon be possible to take up the study of other problems of a plant physiological character.

The importance of maintaining close collaboration with other agricultural and scientific institutions in Sweden and in other countries is emphasized. Most important of all, however, is it to remain in intimate contact with Swedish farmers on whose account in the first place the Association performs its work. (See also p. 275 of this issue.)—R.P.J.

Italian Africa (63)

Agricultural research in Italian Africa is being organized through the establishment of a Royal Agronomic Institute which will be under the control of the Minister for Italian Africa. Through the Institute, the Minister, with the aid of a committee of experts, will direct and regulate the activities of the Agricultural Experiment Stations in the territory. The Institute's functions are outlined in an article by G. R. Giglioli in *Agricoltura colon*. 33. 162-6. 1939. They comprise (1) collection of all information relating to experimental work in tropical and subtropical countries that might be of use under conditions in Italian Africa ; (2) keeping in touch with all problems of interest to the territory, where necessary through research in the Institute's own laboratories or in those of specialists who might usefully co-operate ; (3) collection of experiment material (seeds, plants, etc.) from countries where approximately similar conditions prevail, on an exchange basis. Preparatory studies are already in progress, concerned respectively with the cereals grown in Italian Africa, with its forage plants, the general vegetation, etc. The documentation of work done by experiment stations in tropical and sub-tropical countries is also in progress, and contacts are made with scientific institutes and scientists with a view to the exchange of publications, material and experience. Material for experimental purposes has already been

obtained from the United States, Central and South America, British East Africa, the Belgian Congo, Madagascar, Malay, the Dutch Indies, Japan, and Australia (from which continent forage plants have been obtained). Forage legumes are among the plants to which special attention is being devoted.—G.M.R.

Puerto Rico (729.5)

Proposed Inter-American University

According to *Science* 90. No. 2331. 1939, the report has been published of the commission appointed by President Roosevelt to make recommendations for the proposed establishment of an Inter-American University, consisting of six graduate schools and research units grouped about the University of Puerto Rico, of which they would be an extension but not an integral part. The chairman of the commission was Dr. Isaiah Bowman.

Of the six special service units recommended for inclusion in the programme one is already in existence, namely, the School of Tropical Medicine. The other units would be a Graduate School of Tropical Agriculture, a Graduate School of Economics and Business, Institute of Languages, Literature and History of the Americas, an Institute of Law, and a Tropical Fishery Research Laboratory. The burden of building and supporting the proposed institution must be borne outside Puerto Rico, which is already contributing as much as it can towards the maintenance of the present University. Operating costs are estimated at about $1,250,000 per annum after the Institute has become settled, and during the first few years there would be in addition capital expenditures for erecting and equipping essential buildings.

Responsibility for the undertaking must be assumed chiefly by the United States Government, with as much assistance as possible from private foundations and individuals, and from universities throughout the Americas.

U.S.A. (73)

Dr. O. S. Aamodt

We have to announce the appointment of Dr. Olaf S. Aamodt as Principal Agronomist in Charge of the Division of Forage Crops and Diseases, effective July, 15, 1939. Dr. Aamodt is recognized as being one of the outstanding agronomists of the country. He received the following degrees from the University of Minnestoa : B.S. degree in 1917 ; M.S. degree in plant breeding in 1922 ; and Ph.D. degree in genetics in 1927. He was employed in the Bureau of Plant Industry from September 1, 1916, to June 20, 1917 under temporary appointments, and on July 1, 1917 he was given a probationary appointment as Scientific Assistant in Plant Pathology. He served in various capacities until June 15, 1928, when he resigned as Associate Pathologist to accept the position of Geneticist and Plant Breeder at the University of Alberta, Edmonton, Canada. In May, 1935, he accepted the position as Head of the Department of Agronomy at the University of Wisconsin, a position which he held until his recent appointment as Head of the Division of Forage Crops and Diseases.

Committee on ecology of grasslands in North America

The following is a quotation from ' Some activities of the Division of Biology and Agriculture of the National Research Council ' appearing in *J. Amer. Soc. Agron.* Vol. 31. No. 3. 1939, with particular reference to the work of the above Committee.

" This Committee, of which Dr. V. E. Shelford is chairman, is sponsoring a movement to set aside more or less extensive grassland areas and preserve them for research and as controls against

ordinary methods of utilization in connexion with agricultural and other developments of civilization. Reports growing out of the work of the committee emphasize the necessity for reserving grassland areas comparable in extent and purpose to existing reservations of forest areas in national parks. These reports also list and discuss the kinds of studies of plants and animals, of their interrelations and of their relationships to soils, climate, etc., which might be made possible and be promoted by the reservation of appropriate areas. Two papers have appeared in recent issues of the *Scientific Monthly*, namely, ' The need for research on grasslands,' by H. C. Hanson and C. T. Vorhies, March, 1938 (*Herb. Abstr.* 10. No. 1. 1940) ; and 'Check areas as controls in land use' by H. C. Hanson, February, 1939 [See also *Herb. Abstr.* 9. Abs. 1246, 1939.]

Argentine Republic (82)

The Statutes, dated 8 June, 1936, that govern the organization of the Research Institutes working under the Faculty of Agronomy and Veterinary Science of the University of Buenos Aires, have been published in the form of a booklet [Research Institutes, Statutes governing their creation and organization, personnel and schedules of work. Buenos Aires, 1938, pp. 76.] The Institutes number fourteen ; some are of new creation ; the work of others, for example the Institute of Genetics, founded in 1929, has been incorporated under the 1936 Statutes. Work in progress at the last-named Institute includes the following. (1) *Zea Mays*. Genetical and cytological study, conservation and improvement of testers, breeding for an early bitter maize by the crossing of S. American bitter maize with Colorado Cuarenton, and breeding for self-fertilized lines of commercial varieties ; selection and hybridization including top crosses with good local varieties, and breeding for early forms resistant to insects that attack the cobs. (2) *Poa*. Genetical and cytological analysis of the inheritance of sex and other characters in some species. (3) *Medicago*. The Institute continues to enlarge a collection of material for breeding, comprised of select varieties distinguished by special characters such as resistance to the stem nematode, to *Uromyces alfalfae* and *Peronospora trifoliorum*, good tillering, high yield, etc. Efforts are being made to obtain plants homozygous for nematode resistance.

The Institute for Agricultural Chemistry includes the following among its studies : determination of vitamin A in different varieties of maize, and of vitamin C in other forage crop plants ; chemical study of various wild and cultivated plants used for animal fodder ; soil studies and surveys.—G.M.R.

PRINTED BY THE
CAMBRIAN NEWS (ABERYSTWYTH), LTD.
650/12/39

IMPERIAL BUREAU OF PASTURES AND FORAGE CROPS

HERBAGE PUBLICATION SERIES

This Bureau covers literature on grassland and forage crops, the botanical aspects of soil conservation, and certain plant biological research. It issues two quarterly journals :

Herbage Abstracts. Annual subscription 25s., single parts 7s.

Herbage Reviews. Annual subscription 15s., single parts 4s.

A reduction of 5s. allowed when *Herbage Abstracts* is also ordered.

The Bureau also issues Bulletins and Mimeographed Publications (bibliographies, etc.) at irregular intervals. Particulars of Bulletins 26, 27, 28 and 29 are given below ; details of earlier issues are available on request.

BULLETIN No. 26, PUBLISHED SEPTEMBER, 1939

"Research on grassland, forage crops and the conservation of vegetation in the United States of America"

Compiled by R. O. WHYTE

(An account of current research in the Division of Forage Crops and Diseases, Bureau of Plant Industry, range research in the U.S. Forest Service, the research carried on by the Soil Conservation Service, the U.S. Golf Association, the Carnegie Institution of Washington, and the State agricultural experiment stations.)

Pages 113, maps, indexes of subjects and genera. Price : Five shillings.

BULLETIN No. 27, TO BE PUBLISHED DECEMBER, 1939

"The control of weeds"

Edited by R. O. WHYTE

(A symposium on current research and practice in the eradication of undesirable plants in arable land, grassland, etc., by cultural, chemical and biological means.)

Contributions by : T. K. Pavlychenko and R. H. F. Manske (Canada) ; A. S. Crafts and R. N. Raynor, L. W. Kephart and J. Monteith, Jr. (U.S.A.) ; B. Rademacher (Germany) ; G. A. Currie and A. P. Dodd (Australia) ; E. Bruce Levy and D. Miller (New Zealand) ; D. G. Steyn (South Africa) ; J. C. Luthra (India).

Pages : about 180. Fully illustrated. Price : Seven shillings and sixpence.

BULLETIN No. 28, TO BE PUBLISHED DECEMBER, 1939

"Technique of grassland experimentation in Scandinavia and Finland"

(A symposium on the technique employed in pastures studies, botanical analysis, etc.)

Contributions by : G. Giöbel and K. Lundblad (Sweden) ; B. Sakshaug and H. Foss (Norway) ; H. Bögh and J. Hansen (Denmark) ; C. A. G. Charpentier (Finland).

Pages : about 40. Price : Two shillings and sixpence.

BULLETIN No. 29, TO BE PUBLISHED DECEMBER, 1939 OR JANUARY, 1940

"Grassland and forage crop research in Australia"

(A completely revised and up-to-date edition of Bulletin No. 14 in the same Series. Further details to be issued in due course.)

Price : Five shillings.

IMPERIAL AGRICULTURAL BUREAUX

IMPERIAL BUREAU OF PASTURES AND FORAGE CROPS

(See inside back cover)

IMPERIAL BUREAU OF PLANT BREEDING AND GENETICS

School of Agriculture, Cambridge

This Bureau covers current literature on the breeding, genetics, and cytology of economic plants, including forage crops, fruits, and forest trees, and relevant publications in allied fields, such as applied statistics, plant pathology and other sciences, and issues a quarterly publication.

PLANT BREEDING ABSTRACTS

Annual subscription, 25s., single parts, 7s. 6d.

IMPERIAL FORESTRY BUREAU

39, Museum Road, Oxford

This Bureau covers current literature on all branches of forestry, and issues a quarterly publication.

FORESTRY ABSTRACTS

Annual subscription 25s., single parts 7s. 6d.

IMPERIAL BUREAU OF HORTICULTURE AND PLANTATION CROPS

East Malling Research Station, East Malling, Kent

This Bureau covers current literature on horticulture, including fruit, vegetables, commercial flower production, the cultivation of tropical plantation crops and the storage and processing of horticultural products, and issues a quarterly publication,

HORTICULTURAL ABSTRACTS

Annual subscription 25s., single parts 6s. 6d.

IMPERIAL BUREAU OF SOIL SCIENCE

Harpenden, Herts.

This Bureau covers current literature on soil science, and issues an abstracting journal six times yearly,

SOILS AND FERTILIZERS

Annual subscription 25s., single parts 5s.

IMPERIAL BUREAU OF ANIMAL NUTRITION

Rowett Institute, Bucksburn, Aberdeen

This Bureau covers current literature on the subject of nutrition (human and animal) in all its aspects. Each issue contains a review article by a recognized authority on a subject of general interest.

NUTRITION ABSTRACTS AND REVIEWS

Annual subscription 42s., single parts 13s.

Each Bureau also issues Technical Communications and Bibliographies. Details on application to its Deputy Director, to whom subscriptions to its Abstract Journal should be sent. Concession prices are available for subscribers in Great Britain and other countries of the British Commonwealth. Certain Bureaux publish special editions of their abstract journals printed on one side of the paper only, for use in card indexes.